

BIOSYSTEMATIC STUDIES IN THE  
ARTEMISIA MARITIMA COMPLEX  
IN EUROPE

BY KARIN PERSSON

Lund 1974







BIOSYSTEMATIC STUDIES IN THE ARTEMISIA  
MARITIMA COMPLEX IN EUROPE

AV

KARIN PERSSON

FIL. LIC., MLM.

AKADEMISK AVHANDLING

som för avläggande av filosofie doktorsexamen vid  
Matematisk-Naturvetenskapliga Fakulteten vid Universitetet  
i Lund kommer att offentligens försvaras å föreläsningssalen vid Institutionen för Systematisk Botanik,  
fredagen den 18 januari 1974 klockan 10.00.

Lund 1973

# ACKNOWLEDGEMENT

The present study has been supported by grants from the Swedish Natural Science Research Council, The University of Lund, the Royal Physiographic Society of Lund and the Lund Botanical Society.





# BIOSYSTEMATIC STUDIES IN THE ARTEMISIA MARITIMA COMPLEX IN EUROPE

By KARIN PERSSON

Department of Plant Taxonomy,  
University of Lund,  
Ö. Vallgatan 18--20,  
S-223 61 Lund, Sweden

## ABSTRACT

1. Artemisia maritima, A. vallesiaca and A. santonicum have been investigated cytologically. All species were found to have the basic number of  $x=9$ . A. maritima was observed to be hexaploid, but only c. 65 % of the plants were euploid ( $2n=54$ ). About 23 % were aneuploids ( $2n=50, 51, 52, 53, 55$  or  $56$ ), and the rest, c. 13 %, were aneusomatic with two or three chromosome numbers observed in each root tip. Some regional variation in somatic instability was established. The plants with aberrant chromosome numbers often displayed lowered vitality, a high percentage of meiotic irregularities, and reduced pollen stainability and fruit-setting compared with euploid plants. A. vallesiaca was tetraploid ( $2n=36$ ). Somatic divisions seemed to be regular, and meiosis was also normally regular. In A. santonicum three ploidy levels were observed. Plants from Austria and Czechoslovakia were diploid ( $2n=18$ ), from Hungary and Roumania tetraploid ( $2n=36$ ) and from Greece hexaploid ( $2n=54$ ). Meiotic irregularities and reduced pollen stainability characterized some of the diploids and tetraploids (hexaploids were not studied from this respect).

The morphology of the somatic chromosomes was largely similar in the three species, but A. santonicum had a slightly more asymmetric karyotype. The number and position of satellites varied both within and between populations in all taxa.

2. Morphological variation was studied and compared for A. maritima, A. vallesiaca and A. santonicum. The range of variation was often wide, and overlapping between species great. There were no single diagnostic characters, but it was found necessary to use groups of characters for the description and identification of a species.

3. Intraspecific morphological variation was analysed in A. maritima, A. vallesiaca and A. santonicum. In A. maritima grand populations (groups of populations) from different areas were compared. Some regional racial differentiation was apparent. The populations from Öland and Gotland (Sweden) were particularly characteristic, but the W. Swedish (Bohuslän, Halland) and the German inland (Artern area) populations were also fairly well defined. Differences in the rest of the material were less pronounced. In A. vallesiaca the Swiss and Italian populations were compared, and the differences between them were found to be insignificant. Finally, the three cytotypes of A. santonicum were compared. In most morphological characters there was a fairly distinct dissimilarity between diploids and polyploids. Measurements of pollen diameter were made on extensive herbarium material and this character was found to be of diagnostic value in separating diploids from polyploids.

4. Tolerance to salinity in connection with germination and growth of seedlings was investigated for one population of A. santonicum and four populations of A. maritima. All germinated best in the absence of NaCl, and seedling growth was optimal in a non-saline medium or in salt solutions of very low concentrations, though the seedlings became more salt tolerant with age. Morphological characters



such as pubescence, leaf size, breadth of leaf segment and stomatal length were found to be affected by higher concentrations (1--5 % NaCl).

5. A. maritima, A. vallesiaca and A. santonicum were all found to be self-sterile. Crosses between the species and between different ploidy levels of A. santonicum failed. Populations of A. maritima from 12 areas were crossed reciprocally. Partial reproductive isolation was prevalent in some races, particularly the Öland/Gotland populations (Sweden), versus the rest of the material. Most primary hybrids were intermediate in morphological characters compared with their parents, but in F<sub>2</sub> occasional recoveries of parent-like types were observed.

6. Variation and evolution within the A. maritima complex (A. maritima, A. vallesiaca, A. santonicum, A. lerchiana, A. taurica, A. nitrosa, A. dzevanovskyi, A. fragrans, A. nutans, A. pauciflora and A. caerulescens) are discussed. It is argued that the polyploid species are probably of hybridogenic origin (allopolyploids, possibly of the segmental type). Certain species affinity groups are suggested on the evidence of morphology, chromosome number and distribution. Probable migratory routes of the species, and conditions during Late-glacial and Post-glacial times are discussed.

7. The following taxa are taxonomically revised: Artemisia maritima L. ssp. maritima, A. maritima L. ssp. humifusa (Hartm.) K. Pers. stat. nov., A. vallesiaca All., A. santonicum L. ssp. santonicum, A. santonicum L. ssp. patens (Neillr.) K. Pers. comb. nov., A. caerulescens L. ssp. caerulescens, A. caerulescens L. ssp. gallica (Willd.) K. Pers. comb. nov.

## CONTENTS

|                                                                                                  |    |
|--------------------------------------------------------------------------------------------------|----|
| Introduction.....                                                                                | 1  |
| Part I. <u>Artemisia maritima</u> L., <u>A. vallesiaca</u> All. and <u>A. santonicum</u> L. .... | 3  |
| Material.....                                                                                    | 3  |
| Code of Plant Numbers.....                                                                       | 4  |
| Chromosome Studies.....                                                                          | 5  |
| Chromosome Numbers Previously Published.....                                                     | 5  |
| The Present Investigation.....                                                                   | 6  |
| <u>Artemisia maritima</u> .....                                                                  | 8  |
| Chromosome Number.....                                                                           | 8  |
| Aspects of Aneusomaty and Aneuploidy.....                                                        | 10 |
| Chromosome Morphology.....                                                                       | 18 |
| <u>Artemisia vallesiaca</u> .....                                                                | 21 |
| Chromosome Number.....                                                                           | 21 |
| Meiosis and Pollen Viability.....                                                                | 21 |
| Chromosome Morphology.....                                                                       | 22 |
| <u>Artemisia santonicum</u> .....                                                                | 23 |



|                                                              |    |
|--------------------------------------------------------------|----|
| Chromosome Number.....                                       | 23 |
| Meiosis and Pollen Viability.....                            | 23 |
| Chromosome Morphology.....                                   | 24 |
| Morphology and Morphologic Variation.....                    | 26 |
| Morphologic Characters of Taxa Compared.....                 | 26 |
| Vegetative Development.....                                  | 27 |
| Rhizomes.....                                                | 27 |
| Stems.....                                                   | 28 |
| Leaves.....                                                  | 30 |
| Inflorescence.....                                           | 35 |
| Synflorescence.....                                          | 35 |
| Capitula.....                                                | 38 |
| Floret.....                                                  | 41 |
| Glands.....                                                  | 44 |
| Stamens.....                                                 | 45 |
| Pollen.....                                                  | 46 |
| Pistil.....                                                  | 48 |
| Fruit.....                                                   | 49 |
| Conclusions.....                                             | 50 |
| Variation Within Taxa.....                                   | 52 |
| <u>Artemisia maritima</u> .....                              | 52 |
| Variation at Population Level.....                           | 52 |
| Analysis and Comparison of Variation in Nine                 |    |
| Grand Populations.....                                       | 54 |
| <u>Artemisia vallesiaca</u> .....                            | 69 |
| Swiss and Italian Populations Compared.....                  | 69 |
| <u>Artemisia santonicum</u> .....                            | 71 |
| Diploids, Tetraploids and Hexaploids Compared.....           | 71 |
| Germination and Tolerance to Salinity.....                   | 76 |
| Seedling Development.....                                    | 76 |
| The Effect of Sodium Chloride on Germination and Growth..... | 77 |
| Material Investigated.....                                   | 77 |
| Germination.....                                             | 78 |
| Growth of Seedlings.....                                     | 79 |
| Other Aspects.....                                           | 81 |
| Conclusions.....                                             | 81 |
| Crossing Experiments.....                                    | 84 |
| Methods. Self-sterility.....                                 | 84 |
| Crossing Experiments Between Species.....                    | 84 |
| Crossing Experiments Within Species.....                     | 85 |
| Material.....                                                | 85 |



|                                                                       |     |
|-----------------------------------------------------------------------|-----|
| Fruit-setting After Crossing and Germination of Achenes               |     |
| Obtained.....                                                         | 86  |
| Development and Vitality of Hybrid Plants.....                        | 87  |
| Morphology of Hybrid Plants.....                                      | 89  |
| Meiosis and Pollen Fertility in Hybrid Plants.....                    | 91  |
| Number of Chromosomes in Hybrid Plants.....                           | 92  |
| Fruit-setting and Germination of Achenes Obtained                     |     |
| After Sib-mating Within $F_1$ .....                                   | 93  |
| Development, Morphology and Vitality of $F_2$ Plants.....             | 94  |
| Pollen Fertility and Fruit-setting in $F_2$ Plants.....               | 96  |
| Conclusions.....                                                      | 97  |
| Taxonomy, Distribution and Habitat.....                               | 99  |
| Key to the Taxa.....                                                  | 99  |
| <u>Artemisia maritima</u> L. ....                                     | 100 |
| <u>Artemisia maritima</u> L. ssp. <u>maritima</u> .....               | 103 |
| The West Swedish Form Series.....                                     | 104 |
| The Baltic Form Series.....                                           | 106 |
| The North Sea Form Series.....                                        | 107 |
| The French Form Series.....                                           | 109 |
| The British Form Series.....                                          | 110 |
| The Inland Form Series.....                                           | 112 |
| <u>Artemisia maritima</u> L. ssp. <u>humifusa</u> (Hartm.) K. Pers..  | 118 |
| <u>Artemisia vallesiaca</u> All. ....                                 | 121 |
| <u>Artemisia santonicum</u> L. ....                                   | 125 |
| <u>Artemisia santonicum</u> L. ssp. <u>santonicum</u> .....           | 128 |
| <u>Artemisia santonicum</u> L. ssp. <u>patens</u> (Neillr.) K. Pers.. | 130 |
| Part II. Comments on Variation and Evolution Within the               |     |
| Complex.....                                                          | 135 |
| The Karyotype.....                                                    | 135 |
| Morphologic Variation.....                                            | 139 |
| Speciation and Distribution.....                                      | 145 |
| Literature Cited.....                                                 | 153 |
| Appendix.....                                                         |     |



## Introduction

The genus Artemisia of the tribe Anthemideae/Asteraceae includes more than 200 species, most of which belong to the steppe areas in Eurasia and North and Central America. Four sections or subgenera are generally recognized within the genus, with the following names and synonyms:

- 1) Subgen. Artemisia (Linnaeus 1753 p. 845).  
Syn. (illegitimate): Sect. Abrotanum Besser 1829 p. 222. -- Subgen. Abrotanum (Besser) Rydberg 1916 p. 259.
- 2) Subgen. Absinthium (DC.) Rydberg 1916 p. 257. -- Sect. Absinthium De Candolle in Lamarck & De Candolle 1805 p. 189.
- 3) Subgen. Dracunculus (Besser) Rydberg 1916 p. 251. -- Sect. Dracunculus Besser 1835 p. 16 (illegitimate).  
Syn.: Sect. Oligosporus Cassini 1817 p. 33.
- 4) Subgen. Seriphidium (Besser) Roy 1903 p. 298. -- Sect. Seriphidium Besser 1829 p. 222.

Only one or two morphological characters are used for subdividing the genus into these subgenera which are probably not natural groupings, as is indicated by the many examples of very similar species differing only in the character separating two subgenera. For instance, in his study of Seriphidium in North America Ward (1953) also included Artemisia bigelovii of Artemisia because of its apparent affinity to members of Seriphidium. Some authors have grouped Artemisia, Absinthium and Dracunculus together in one section (Godron in Grenier & Godron 1850) or subgenus (Roy 1903), while others have perhaps more naturally grouped Artemisia and Absinthium together in one section (Gray 1884) or subgenus (Krasheninnikov 1946).

Seriphidium is distinguished from other subgenera in having homogamous capitula, i.e. zygomorphic "ray" florets are lacking. The species concept in the subgenus has varied considerably from time to time. Although Linnaeus (1753) described 3, Stechmann (1775) 7 and Willdenow (1803) 12 Eurasian species later to be comprised in the subgenus Seriphidium many authors later chose to include most Eurasian species as subunits (mostly varieties) within one collective species, Artemisia maritima L. Thus Besser (1834) recognized 20 and Ledebour (1845) 9 varieties (plus many subvarieties) within A. maritima. Only more recently have a number of the taxa within A. maritima



s. lat. again been recognized as distinct species, above all by Russian authors. For instance, Poljakov (1961) recognizes 7 species for the European part of the Soviet Union, while Leonova (1970) in a study of Seriphidium from the same area includes the following 13 species:

|                                              |                                      |
|----------------------------------------------|--------------------------------------|
| <u>A. maritima</u> L.                        | <u>A. taurica</u> Willd.             |
| <u>A. lerchiana</u> Web. ex Stechm.          | <u>A. compacta</u> Fisch. ex DC.     |
| <u>A. nutans</u> Willd.                      | <u>A. pauciflora</u> Web. in Stechm. |
| <u>A. dzevanovskiyi</u> Leonova              | <u>A. gracilescens</u> Krasch. &     |
| <u>A. fragrans</u> Willd.                    | <u>Ilin</u>                          |
| <u>A. santonica</u> L. ( <u>santonicum</u> ) | <u>A. terrae-albae</u> (Krasch.)     |
| <u>A. nitrosa</u> Web. ex Stechm.            | <u>Krasch.</u>                       |
|                                              | <u>A. lessingiana</u> Besser         |

Some of these species (A. fragrans, nitrosa, compacta, pauciflora, gracilescens, terrae-albae and lessingiana) are found only in the south-eastern part of European Russia, entering Europe from Turkey, Sibiria or Kazakhstan. Many species in the list (above all the eight first-mentioned) show clear affinities to each other in a reticulate pattern and thus comprise a so-called species complex. To this Artemisia maritima complex should also be added three central and southern European species, viz., A. vallesiaca All., A. gallica Willd. and A. caerulea L.



PART. I. ARTEMISIA MARITIMA L., A. VALLESIACA ALL. AND  
A. SANTONICUM L.

Material

This investigation is based on spontaneous material of Artemisia maritima, A. vallesiaca and A. santonicum grown under uniform conditions in the Lund Botanical Garden. The material has mainly been collected in the form of living plants, five to fifteen from each locality, which have all been analysed. In some cases plants have been grown from achenes received from other collectors. A list of localities is given in the appendix.

The experimental material was planted in pots in a mixture of one part leaf mould, one part peat mould and one part sand. Fertilizer was added during the first part of the vegetative period. The plants were repotted once a year.

The differences that remain between the plants after at least one year are considered to have a genetical basis. It must be pointed out, however, that the phenotypes obtained from a given genotype in cultivation in several cases may deviate from those obtained under natural conditions. Whenever there is a marked discrepancy between the cultivated plants and the phenotypes generally seen in nature this will be commented upon in the text.

All morphological data given in the taxonomic section are based partly on the author's collections in the field and partly on herbarium specimens from different geographical areas, on loan from the following Herbaria (abbreviations in accordance with Lanjouw & Stafleu 1964): BM, BR, C, CL, COI, E, FI, G, GOET, H, HAL, JE, K, L, LD, LE, LISU, LY, M, MPU, P, PR, PRC, S, SOM, TO, TU, U, UPS, W and WU. As the material is fairly extensive, the data given probably cover most of the range of modification met with in nature.

Morphological terms are according to Lawrence (1951). Geographical names follow the spelling in the Times Atlas (Bartholomew 1955, 1956).



Code of Plant Numbers

The collection from each given locality has been given a number (e.g. 1, 2, 101, 102). The different plants in the locality have been numbered and this number is added to the collection number. The last figure in each plant number is the number of the clone plant, if the original plant has been divided between several pots. For example:

|         |       |                   |
|---------|-------|-------------------|
| 48-11-2 | means | coll.no. 48       |
|         |       | plant no. 11      |
|         |       | clone plant no. 2 |







Kawatani & Ohno 1964

(A. salina Willd., A. monogyna W. & K.)

2n=36

Tarovsky 1948

(A. maritima L.)

Kawatani & Ohno 1964

(A. maritima L. var. patens Neilr. and var. salina Koch, A. salina Willd., A. monogyna W. & K.)

A. maritima L. s. lat.

2n=18

Weinadel-Liebau 1928

2n=36

Titova 1935

Suzuka 1952

Khoshoo & Sobti 1958

Koul 1964

2n=54

Suzuka 1949, 1950, 1952

Suzuka & Koriba 1949

Kawatani 1950, 1952

Kitamura 1957

Khoshoo & Sobti 1958

A. monogyna W. & K.

2n=54

Mitsuoka 1961

## THE PRESENT INVESTIGATION

The immediate aim of this investigation was to determine the chromosome numbers of all the plants studied taxonomically and if possible to make a detailed study of the chromosome morphology. The latter proved to be somewhat difficult, owing to the moderate size of the chromosomes and the mostly high ploidy level. However, other interesting problems turned up in the course of the investigation. The discovery of aneusomaty in A. maritima motivated a more detailed study of the degree of meiotic and somatic instability in this species. Meiosis was also studied in all three species with the aim of setting the degree and type of irregularity in relation to ploidy level and to the degree of vegetative propagation of the respective



species.

The basic number of  $x=9$  was confirmed for the whole material.

## Methods

The somatic chromosomes have been studied in root-tip mitoses. The preparations were made using either of the following two techniques.

1) The plant was kept overnight at a temperature of  $5^{\circ}\text{C}$  and the root tips were fixed in the Svalöf modification of Navashin-Karpechenko. The material was embedded in paraffin wax and sectioned at  $12\mu$ . Before staining the slides were pretreated for 6--12 hours in a 7.5 % solution of citric acid. The sections were then stained in 1 % crystal violet and 2 % aniline solution (2 : 1) for 25 minutes.

2) The preparations were made according to a modification of the method described by Östergran & Heneen (1962). The root tips were pretreated in a 0.2 % aqueous solution of colchicine for two hours and then fixed in Carnoy (3 parts absolute alcohol : 1 part glacial acetic acid). After hydrolysis for 8 minutes in 1-N HCl at  $60^{\circ}\text{C}$  they were stained with Feulgen for 1--2 hours. The roots were softened in 5 % pectinase for two hours and then squashed in a droplet of 45 % acetic acid.

Method no. 1 proved to be most suitable for chromosome counts, while preparations made according to method no. 2 were used for investigating chromosome morphology.

Meiosis was studied in squash preparations. Young buds were fixed in Carnoy for one hour. The anthers were then stained and squashed in a 3 % solution of acetoorcein.

The degree of pollen fertility was estimated by determining the percentage of morphologically well-developed pollen stainable in cotton blue, which of course only gives a rough estimate, possibly a maximum value, of the frequency of actually functional pollen grains. However, in the taxa investigated the correlation between pollen stainability and male meiotic irregularities seems to be good, in the sense that in plants with a proportionately high percentage of meiotic irregularities the value of the pollen stainability was practically always low.



## ARTEMISIA MARITIMA

Chromosome Number

About 900 plants (110 populations) from the coasts of north-western Europe (Sweden to France) and one inland locality (a saline area near Artern in central Germany) have been investigated (2--3 plates per plant). All plants were hexaploid, which confirms the earlier reports of counts made by Kawatani & Ohno on material from Sweden, Denmark, the Netherlands, Great Britain and central Germany, and by Gadella & Kliphuis on material from the Netherlands.

However, in the present investigation only c. 65 % of the plants were observed to be wholly euploid ( $2n=54$ ) (Fig. 1 A). About 23 % were aneuploids, and the aberrant numbers found were  $2n=50$ , 51, 52, 53, 55 and 56 (Fig. 1 B--G), of which the even number 52 and then the number 53 were the most frequent (Table 1). Only one case of variation of the chromosome number around the euploid number has been reported before in Artemisia, by Shimotomai (1947) for A. montana ( $2n=51$ , 52, 53 and 54). This species, however, does not belong to the same subgenus as the species group in this investigation. Furthermore, Shimotomai does not mention if the variation in number is inter- or intra-individual or both, which would have been of great interest as in the present investigation the phenomenon of different chromosome numbers occurring not only within the same plant but also within the same root was discovered in c. 13 % of the material. Duncan (1945) has suggested the term aneusomaty for the occurrence of different chromosome numbers within tissues of the same organism. In the aneusomatic plants of Artemisia maritima there was usually a difference of 1 or 2 between the numbers found in a single individual, e.g. 52 and 53, 52 and 54, 54 and 55 (Fig. 2). Only rarely were more than two numbers observed.

The euploid number (54) was also the most frequent in the intra-individually varying plants (Table 1). Among the aneuploid numbers, it is to be noted that the numbers immediately next to 54, viz. 55 and in particular 53, are more frequent than the even number 52, unlike the non-aneusomatic material where 52 probably represents the most stable cytotype beside the euploid condition.

For the material as a whole 54 is found in about 74 % of the plants.



Only 13 populations were observed to be totally euploid, but even this may not be true as only 5--15 individuals in each population have been examined. In four populations no euploids at all were observed, viz., coll. no. 47 Nordkoster, Bohuslän, Sweden, coll. no. 57 Jerup, Jylland, Denmark, coll. no. 58 Lyngså, Jylland, Denmark, and coll. no. 129 Cabourg, Calvados, France.

Aneuploidy and aneusomaty seem to be rather evenly distributed in large parts of the area of distribution (Table 2). On Öland and Gotland (Sweden) the percentage of aneusomatic plants is somewhat higher than the average, and similarly aneuploids are commoner in France than elsewhere. Moreover, there is a strikingly lower percentage of aberrants in Great Britain and in the only inland locality, Artern in central Germany (in the latter case the material is limited, however, so it is difficult to draw any definite conclusions). It is remarkable that there seems to be no correlation between the frequencies of aneuploidy and aneusomaty. Thus, on Öland/Gotland a high percentage of aneusomatics is found together with average frequencies of aneuploids, while in France there is an average frequency of aneusomatics together with a high frequency of aneuploids. In the author's opinion the frequency of aneusomatic plants is probably somewhat higher everywhere than shown in Table 2, owing to the fact that only two or three plates have been counted in each individual, and there is no guarantee that another number would not turn up in the next count. The frequencies found are undoubtedly not far wrong, however, as aberrant chromosome numbers have been found to correlate strongly with irregular somatic and meiotic divisions, lowered plant vitality etc. as will be shown later in this section. Consequently the existence of some local variation in somatic instability can be established. No correlation has been found, however, between the frequency of aberrant plants and population size.

In a few cases, root-tip cells with unusually high chromosome numbers were found scattered among the hexaploid cells. These cells often had double the hexaploid number, i.e. approximately 100 chromosomes, the phenomenon thus being a case of endopolyploidy.



## Aspects of Aneusomaty and Aneuploidy

### Somatic Disturbances

In aneusomatic and aneuploid plants several cases of disturbed somatic division have been observed. These are not confined to a single layer in the root but seem to be distributed throughout all the root histogens. Disturbances usually occur as bridges, often with a sticky appearance, in anaphase plates (Fig. 3), less usually lagging chromosomes are to be seen outside metaphase plates or between anaphase groups. Separation difficulties between daughter chromatids probably sometimes lead to the fragmentation of chromosomes. Such fragments have been observed though admittedly very rarely.

### Plant Vitality

The aberrant genetic conditions are apparently not detrimental to any great extent. Genetic aberrations are not usually found to be harmful in taxa with a high degree of polyploidy, as there is a great deal of duplication of genetic material in polyploids which therefore can tolerate the loss of one or more chromosome pairs. Furthermore, there seems to be a chance for structural mutations to survive and even accumulate in species with an effective form of vegetative propagation as in Artemisia maritima.

However, although the aberrants probably survive for a long time in wild populations under natural conditions, a certain reduction in vitality is apparent under more deviating conditions, for instance in cultivation. The percentage of aneusomatic and aneuploid individuals among plants in cultivation was examined for three years , 1) in those flowering each year and 2) in those that died during the whole period. It was obvious that the aberrant genetic conditions had a negative effect on plant vigour. The percentage of aberrants among the plants that flowered was always much lower than the corresponding percentage among those that did not flower (Table 3). This was shown statistically in a  $\chi^2$  analysis of the results for one year (year 3; <sup>xx</sup>significance). During this year about 67 % of the euploids developed flowering shoots but only approximately 57 % of the



aberrants did so. Among these it was obvious that aneuploidy had a greater effect on plant vigour than aneusomaty, as only c. 55 % of the aneuploid plants flowered, of the aneusomatics, however, 60 % (Fig. 4). About 60 % of the plants that died during the three years were aberrants, whereas in the entire material only c. 35 % are aneuploid or aneusomatic. Consequently, a considerably larger proportion of aberrant plants die in cultivation soon after planting, or, at least, never reach flowering.

### Male Meiosis

Meiosis was studied in 11 euploid and 26 aberrant plants.

Male meiosis in euploids is usually regular, with 27 bivalents formed at metaphase I. Not infrequently some univalents and also one or two multivalents are found. Some disturbances have been observed in later stages, e.g. bridges and laggards at anaphase I and, rarely, at anaphase II. The frequency of disturbed divisions in such cases is less than one per cent.

In the aneuploid and aneusomatic plants meiotic irregularities are the rule rather than the exception. Disturbed male meioses have been found in about 90 % of these plants. Disturbance frequency in totally aneuploid individuals is usually approximately 2--7 % at first meiotic division (anaphase--telophase I) and 2--11 % at second meiotic division (anaphase--telophase II). A tendency towards greater stability can be discerned in plants with the chromosome number 52. In several of these individuals no disturbances at all have been observed. Aneusomatic plants containing euploid cells also seem to be somewhat less instable. The corresponding figures for such plants are c. 2--5 % and c. 2--3 %, respectively.

Table 4 summarizes the disturbances at first and second meiotic division in some aneuploid and aneusomatic plants. A description of some stages of meiosis in aberrant plants follows below.

DIAKINESIS AND METAPHASE I. Most PMCs were rather difficult to analyse. In good preparations it could be seen that most of the configurations were bivalents, some rod-shaped, and that some obviously formed only loose associations. Univalents were frequently found, up to 8 in number, at metaphase often lagging outside the plate (Fig. 5 A). There was a certain lack of pairing and a low chiasma frequen-



cy (less than one per arm). In most preparations at least one multivalent was present, often two or three, usually in the form of tri- or quadrivalents, rod-shaped or of a more complicated structure. Some of the configurations (possibly satellite chromosomes) in diakinesis seemed to be associated with the nucleolus.

ANAPHASE I. Failure to pair initially obviously results in lagging and a random passage of the univalents to one or other of the poles at anaphase, a varying number of such lagging chromosomes being observed at this stage (Fig. 5 B, C). Sometimes division is upset to a high degree with whole groups of chromosomes lagging, resulting in dyads with additional micronuclei (Fig. 5 D) or consisting of one very large and one small nucleus (Fig. 5 E, F). A large number of these abnormal products of division apparently degenerate.

Bridge formation accompanied by fragments was also found in many cases (Fig. 5 H). The formation of bridges and fragments can be explained in several ways. It may be the result of crossing-over within heterozygous paracentric inversions. Another explanation is that bridge and fragment formation arises from random chromatid breakage and reunion processes in prophase, in which case there should be differences in the size of the fragments (cf. Lewis & John 1966). Because of the small size of the fragments it was not possible to decide which of these two alternatives was relevant. However, it can be presumed (cf. Stebbins 1950 p. 83) that most inversions occurring in plant species are small in proportion to the chromosome size so that in species with small chromosomes they will seldom form chiasmata when paired with a normal segment. The small chromosome size in Artemisia maritima in combination with the frequent lack of pairing and low chiasma frequency does not make it seem likely that the rather high frequency of bridge and fragment formation is the result of crossing-over in structurally heterozygous plants alone. Probably some processes of breakage and reunion of chromatids are also involved.

A third explanation of bridge and fragment formation, involving an E-type bridge with a fragment the size of an entire chromosome which would be the result of crossing-over in a non-inverted segment translocated from one chromosome arm to the other (cf. Brandham 1969), does not seem to apply to the current material. The fragments always seemed to be smaller than the chromosomes.

The bridges were sometimes ruptured and various parts of the chromatids would then be incorporated in either dyad nucleus. Very often, however, the bridges persist and can be seen in all the following stages.

METAPHASE II. The disturbances at second meiotic division were frequently even more pronounced than at first meiotic division. At metaphase single chromosomes or groups of chromosomes could often be seen lagging outside the plates (Fig. 5 I, J).

ANAPHASE AND TELOPHASE II. Both bridges and lagging chromosomes (Fig. 5 K, L) or groups of chromosomes were observed, the latter giving rise to one or more micronuclei of varying size (Fig. 6). The tetrads did not often deserve their name, as they could contain as many as six or seven nuclei, often of different size. Many of these abnormal tetrads apparently degenerated. If the whole second division is upset, it may lead to non-disjunction or lagging of the whole chromosome set in each dyad nucleus. The product would then be two restitution nuclei, each forming an unreduced gamete (Fig. 6 D). The resulting pollen grains would be more or less double the size of normal grains. Such "giant" pollen grains were observed in a few plants (Fig. 53 B, D). Similar cases of unreduced giant pollen grains have been reported in some other polyploid species with irregular meiosis, e.g. Rorippa sylvestris (Jonsson 1968) and Caltha palustris (Reese 1954).

The giant pollen grains could of course also be the result of a break-down of the first division with a subsequent division into two daughter nuclei. As mentioned before such cases of more or less collapse at anaphase I have been observed (Fig. 5 F).

The bridges were mainly ones that had persisted after anaphase I, but new bridges were also formed. In several cases the bridges did not break even at pollen formation (Fig. 6 F). Uninucleate pollen could be seen with their nuclei connected through proboscis-like projections. Pollen-wall formation sometimes failed between such connected pollen grains resulting in "twin" pollen grains. Such pollen grains were also reported by WeipedeL-Liebaw (1928) for another Artemisia species with highly irregular meiosis, viz. A. dracunculus.

Some of the above-mentioned disturbances may also have arisen from structural rearrangements in the form of translocations, but as the prophase stages (e.g. pachytene) are very difficult to analyse in this material, it is not possible to form any definite conclusion as to the frequencies of translocations (if any) in relation to inversions or other breakage and reunion phenomena.



### Pollen Viability and Fruit-setting

Pollen viability was determined as the percentage of well-developed pollen grains stainable in cotton blue. Two counts of 200--300 grains in each on different occasions were made for each plant. As the two counts were only slightly divergent it may be assumed that the pollen stainability is modificatively variable to only a slight extent.

The fertility of the pollen is of course affected by the irregular meiotic conditions. As was mentioned previously a large number of the abnormal tetrad cells degenerate at an early stage, but many of them probably develop into pollen grains, a high percentage of which are not viable. In the euploids usually 80--95 % of the pollen grains stained with cotton blue and were apparently well-developed, while the percentages obtained in the aneuploid and aneusomatic plants were much lower (Fig. 7). It is worth noting that pollen stainability in aneusomatic plants containing euploid cells was somewhat higher than in the totally aneuploid plants.

It is significant that the pollen viability values observed were usually distinctly lower than the frequencies of normal meiotic divisions. Much of the pollen sterility noted in Artemisia maritima might be caused by genic or cryptic structural factors with no visible effect on meiosis.

On the female side there is likewise a marked reduction in fertility in the plants with aberrant chromosome numbers. Among these fruit-setting (interpreted as number of achenes/number of apparently well-developed flowers) was usually only about 20--50 %. In the euploids fruit-setting was often as high as 60--80 %.

It is to be noted that these values were obtained in cultivation with controlled pollination. In nature fruit-setting does not often attain the above-mentioned values. The fact that achenes are rarely produced is even mentioned in some floras, e.g. Clapham, Tutin & Warburg (1962). Much of the sterility in nature is probably connected with strong self-incompatibility in association with the extensive growth of single clones.

## Discussion

The phenomenon of intra-individually variable chromosome numbers, or aneusomaty (Duncan 1945), has been observed in a number of wild plant species, e.g. Claytonia virginica (Lewis 1962, 1967), Cardamine pratensis (Berg 1967) and Plantago coronopus (Gorenflot 1968). Some reports of aneusomaty refer to experimentally obtained polyploids, e.g. tetraploid Ribes nigrum (Vaarama 1949) or hybrids, e.g. in Godetia (Håkansson 1950). However, the majority of the cases of intra-individual aneuploidy seem to be wild or cultivated plants with extensive vegetative propagation such as Begonia (Sharma & Bhattacharyya 1957, Meyer 1965), Hymenocallis (Snodad 1955) and various other species within monocotyledonous families (Liliaceae, Amaryllidaceae, Araceae: Sharma 1956). Nardus stricta, another example (Rychlewski 1967) is even agamospermous. Sharma (1956) comes to the conclusion that aneusomaty is especially common in plants that propagate vegetatively. The case of Artemisia maritima supports this theory.

According to Ehrendorfer (1959 a) it is possible to distinguish two main groups of intra-individual aneuploidy. In the first case, there is usually a significant oscillation around the euploid number -- predominantly a reduction, as in A. maritima. Chromosome variation is found in both generative and vegetative tissues. There seems to be no connection with spontaneous aberrations in meiosis. This group consists almost exclusively of polyploids; in particular young or experimentally produced taxa.

The second group contains species with weakly oscillating, mostly increasing chromosome numbers. A high rate of spontaneous chromosome aberrations is significant such as stickiness, chromosome breakage, bridges and fragments, and non-disjunction. Cells with varying chromosome numbers are found in generative tissue in particular, e.g. in PMCs resulting from instability in premeiotic mitoses. There is a predominance of diploids in this group, but polyploids also occur (often hybrids).

However, there are several transitional types, as is also admitted by Ehrendorfer. Thus, I do not think that a high frequency of spontaneous chromosome aberrations is characteristic only of the second group. Such aberrations are probably frequent in both groups, though many of the authors mentioned have not discussed meiosis. Particularly in polyploid species with vegetative propagation both somatic and meiotic instability seems to be common, e.g. in Caladium bicolor



(Sharma 1956) and the material examined in the present work, Artemisia maritima. Furthermore, the difference in magnitude of oscillation in chromosome number between the two groups, with a reduction in number chiefly in the first group, is of course a direct consequence of the ploidy level. A loss of one or more chromosome pairs in polyploids (group one) is normally not harmful owing to duplication of genetic material, whereas it would probably mostly be lethal in diploids (group two).

The intensity of somatic instability varies in different material. In Claytonia virginica (Lewis 1962) 7.2 % of the plants investigated had intra-individually variable chromosome numbers, as compared with c. 13 % in Artemisia maritima, while almost all plants of Nardus stricta investigated (Rychlewski 1967) were aneusomatic. As in Artemisia maritima, the euploid number seemed to be the most frequent in most material, but not in Plantago coronopus (Gorenflot 1968), where  $2n + 1$  was the dominant number. In Nardus, as in Artemisia, some populations were recorded with no observation of the euploid number at all. No other local variation in chromosome number seems to have been observed, except in Artemisia maritima as described earlier in this paper and in Plantago coronopus (Gorenflot), in which populations from certain areas were reported with an especially high degree of aneusomaty, sometimes even with four different numbers in the same individual.

As regards the origin of aneusomaty it is probable that some aneuploid gametes resulting from irregular meiosis (e.g. lack of pairing, lagging of unpaired chromosomes) are occasionally functional, and when such gametes combine they will give rise to individuals that risk being cytologically unstable. As Lewis (1962) points out, the greater the numerical disparity between the gametic chromosomes forming a new individual, the greater the chance that the plant will be unstable. When this disparity has reached a certain limit, cell division is thrown out of balance. Bridges and laggards in root-tip mitoses were for instance recorded in Nardus (Rychlewski 1967), as were fragments, a phenomenon also observed in Godetia (Håkansson 1950) and Caladium (Sharma 1956). Many instances of abnormality in the function of the spindle during mitosis have been reported, as in Godetia and Begonia (Meyer 1965). All these types of aberrations in root-cell divisions were in fact found by the present author in Artemisia maritima, albeit in low frequencies.

There are probably several causes contributing to the high degree

of meiotic instability in A. maritima. It has often been shown that chromosome behaviour at meiosis is affected by genic factors as well as by structural differences (Darlington 1932, Rees 1961, John & Lewis 1965). The possibility cannot be excluded that at least some of the meiotic irregularities found in A. maritima are genically controlled. Much structural heterozygosity is also apparent, e.g. for inversions, as indicated by the high frequency of bridge and fragment formation at anaphase I. Several reasons for this accumulation of structural changes can be pointed out. For instance, A. maritima is a hexaploid. The duplication of genetic material in polyploids makes it possible for such plants to stand even a great amount of structural changes. Likewise, being a clonal perennial A. maritima is able to survive despite significant reduction in fertility each year. A third contributing factor to the cytologic instability is the fact that A. maritima is a cross-fertilizer. Münzing (1945) observed that structural heterozygosity is most frequent in outbreeding plants, and it has also been reported numerous times for such species, e.g. Achillea millefolium complex (Ehren-dorfer 1959 b), Elymus rechingeri (Heneen & Runemark 1962). What is more, a certain amount of inbreeding in outbreeding species seems to favour the survival of structural changes, as described for e.g., Campanula (Darlington & La Cour 1950), Oenothera (Cleland 1949), Elymus (Heneen & Runemark 1962) and Leopoldia (Bentzer 1972). Artemisia maritima often occurs in rather large clones. It is to be supposed that most of the neighbouring plants originate from achenes from the same clone, as the majority of the achenes produced by a maternal plant are probably dropped and germinate fairly close to the parental clones. Furthermore, it has been shown, for instance, by Colwell 1951 (in Pinus) that even in wind-pollinated plants (cf. A. maritima) most of the pollen is not carried far from the source, in Pinus up to a distance of 10 to 30 feet. The dispersal patterns of achenes and pollen in combination with the clonal structure will, in A. maritima, probably result in cross-pollination chiefly between sister plants, and consequently, a certain amount of inbreeding is inevitable.

The reasons for the preservation of structural heterozygosity stated above may not be the only ones. Structural rearrangements may sometimes be associated with gene combinations of selective value, and selection will then act to preserve the heterozygous rearrangements as these prevent the favourable combinations from breaking down (cf. Darlington & La Cour 1950).



In Artemisia maritima the unstable cytological conditions in aneuploid and aneusomatic plants were found to have a negative effect on plant vigour, at least under unnatural conditions such as in cultivation. There is no report of a similar effect in other aneusomatic plant species. To a certain extent a parallel may perhaps be drawn between the aneuploid material and conditions found in monosomics and other species with one or a few chromosomes missing or duplicated. Such plants also usually originate from aneuploid gametes resulting from low chiasma frequency and lack of pairing with a subsequent lagging of unpaired chromosomes. However, in such cases it is often so that some chromosomes are more involved in the formation of monosomics etc. than are other members of the complement, whereas in the aneusomatic Begonia (Meyer 1965), for example, and in Nardus (Rychlewski 1967) the whole chromosome set contributes to the aneuploidy. In nullisomic and monosomic individuals of the hexaploid Triticum aestivum (Sears 1944, 1954), for example, a certain reduction in vigour is observed though varying in extent. Trisomes and tetrasomes seem to have less effect on viability. In diploids, such as Datura (Blakeslee 1930) and Drosophila (cf. Swanson 1965 p. 190) the imbalance created by chromosome duplication or, even more, chromosome loss, is less easily withstood and is often deleterious.

### Chromosome Morphology

The absolute length of the somatic chromosomes varies from about 2--3  $\mu$  for the shortest chromosomes to about 4--5  $\mu$  for the long ones with the fixative used. Most of them have submedian centromeres, some, usually including the second largest pair, nearly median, but there is also a rather distinct group of five to six pairs of chromosomes with subterminal centromeres (Fig. 8).

Secondary constrictions are often observed, at least in squash preparations. The satellites are usually borne at the end of the short arm of the chromosomes with a subterminal centromere. Differences in the morphology of the satellite chromosomes exist both within and

between populations, even when only euploid plants are considered, the differences including both the number and size of the satellites and the conspicuousness of the secondary constrictions in presumed homologues. In many preparations some of the satellites have probably more or less fused with the chromosome arms, thus making the constrictions invisible. In some preparations (even using the squash technique) not a single satellite can be observed. That the observed variation in satellite number is real to a certain extent and not solely the result of the preparation technique (different degree of contraction etc.), has been indicated by crossing experiments, through a comparison of the number of satellites in  $F_1$  and parent plants (Table 5). It seems that there are actually no satellite chromosomes at all in some of the parent plants and in some instances there is only one. On the other hand, in some plants as many as five pairs of satellite chromosomes can be distinctly seen.

A certain variation pattern in satellite variation can be discerned if the whole area of distribution is considered. Plants from the coasts of Sweden and the Danish islands have chromosome sets with many satellites, up to 10 in number (in squash preparations; in microtome-cut paraffin preparations a maximum of four satellites can be discerned). Particularly in the Bohuslän--Halland area (western Sweden) the frequency of individuals with a large number of secondary constrictions is high: about 45 % of the plants were observed to have satellites on 8--10 chromosomes of the set. In Skåne (south-western Sweden) the corresponding frequency was about 14 %. On the North Sea coasts of Denmark, Germany and the Netherlands the plants investigated usually had at the most three or four satellites per set, and there was a relatively large proportion of individuals with no secondary constrictions at all (c. 70 %). Similar conditions were apparent in Great Britain, but in France the frequency of satellited chromosomes was again high: only 15 % of the plants had plates (squash preparations) devoid of satellites (as compared with c. 40--50 % in the rest of the material except the North Sea populations). About 54 % had chromosome sets with 6--8 satellited chromosomes. In the material from Artern (central Germany) up to 7 satellites per set were observed.

Owing to the moderate size and the small differences in morphology of most of the chromosomes it is difficult to draw any conclusions as regards the number of morphologically similar chromosome sets present, which would perhaps provide evidence as to the nature of the polyploidy in the species. An attempt has been made (Fig. 8)



to organize the chromosomes in pairs according to size from the largest to the smallest. At least it can be observed that there seems to be only one pair of some chromosome types, whereas there are perhaps more than one pair of other types. Such observations should be interpreted with great caution, however. It has often been shown, for instance in Paeonia (Stebbins 1938) that chromosome sets which look almost identical may in fact differ in structural rearrangements. Results obtained from meiosis should be interpreted with similar caution. The dominance of bivalents with occasional occurrences of tri- or quadrivalents in Artemisia maritima would suggest that the species is an allopolyploid of the segmental type as described by Stebbins (1947). The possibility of autoallohexaploidy cannot be excluded either, although a higher frequency of multivalents in meiosis would then be expected. No definite conclusions can be drawn, however, owing to the difficulties which have often been shown to accompany the interpretation of meiotic chromosome associations. Polyploids have been observed containing three or more identical genomes but nevertheless forming mostly pairs at meiosis (Müntzing & Prakken 1940). Likewise, there exist undoubted allopolyploids in which a large number of multivalents are usually formed (Stebbins 1947). That a rather extensive duplication of chromosomal material is inherent in A. maritima, however, is suggested by the fact that apparently viable gametes of varying chromosome numbers are produced from time to time, as well as morphologically normal plants in which as many as four chromosomes are missing. In view of these facts and the results from the studies on meiosis and chromosome morphology as discussed above, the most likely hypothesis seems to be that Artemisia maritima is a segmental allopolyploid.

## ARTEMISIA VALLESIACA

### Chromosome Number

About 200 plants from mountain slopes (altitude 500--700 m) in the Rhone valley, Switzerland (12 populations) and the Aosta valley, Italy (2 populations) have been investigated. All were tetraploid,  $2n=36$  (Fig. 9), which is in accordance with a previous report on Swiss material by Kawatani (1952). No aneuploid plants have ever been observed by the author. Somatic divisions studied in root tips seemed to be regular.

### Meiosis and Pollen Viability

Male meiosis as studied in about 40 plants was usually regular, 18 bivalents being formed at metaphase I. Occasionally some univalents and/or a trivalent or quadrivalent were found in some cells. Laggards and bridges with fragments at anaphase I have been observed in a few cases, the latter possibly being the result of crossing-over in plants heterozygous for paracentric inversions. Divisions at anaphase II were usually regular except in three plants in which bridges were recorded for a few cells, and ten plants with occasional lagging chromosomes or chromosome groups. The latter resulted in the formation of micronuclei and uninucleate pollen of varying size. One case of giant pollen grains was recorded, a possible product of restitution nucleus formation. On the whole, however, genetic conditions seemed to be much more stable in this species than in Artemisia maritima. It is worth noting that reproduction through vegetative propagation is significantly less pronounced in A. vallesiaca. In comparison with A. maritima the balance between vegetative and sexual reproduction seems to be shifted more towards the latter method.

The percentage of well-developed pollen grains is usually 75--85 % (Fig. 10). Lower values were found in plants with irregulari-



ries observed at meiosis, vary around 82 %. It seems that some of the pollen sterility in A. vallesiaca, as in A. maritima, is caused by genic or cryptic structural factors with no apparent effect on meiotic division as the pollen stainability frequencies recorded were practically always lower than the percentages of regular meiotic divisions.

### Chromosome Morphology

The somatic chromosomes of Artemisia vallesiaca are more or less similar to those of A. maritima both in size and general appearance. The absolute length varies with the pretreatment and fixative used between 2--3 and 4--5  $\mu$ . The majority of the chromosomes are submetacentric or nearly metacentric. At least two or three pairs are in different preparations distinctly asymmetric, with more or less subterminal centromeres. The short arms of these chromosomes are often satellited. Satellites vary both in size and number. More than a third of the plants have two satellites visible in squash preparations, but three, four or even six secondary constrictions are not unusual either (in microtome-cut paraffin preparations a maximum of four satellites are visible). The frequencies of individuals with different numbers of satellites seem to be much the same in Swiss and Italian populations.

In some plants chromosomes with very large satellites have been observed (Fig. 11 5, second pair in second row). The secondary constriction, in some preparations faint but in others very distinct, was in these cases in the middle of the short arm of a submetacentric chromosome.

As most of the chromosomes are much alike in both size and gross morphology it is hardly possible to establish the number of superficially (if not genetically) similar chromosome sets present. At least one easily recognizable chromosome type, however, the most asymmetrical one (often satellited), is only represented by one pair of chromosomes (Fig. 11, pair no. 9).

## ARTEMISIA SANTONICUM

### Chromosome Number

About 100 plants from saline areas in Austria (7 populations), Czechoslovakia (1 population), Hungary (1 population), Roumania (2 populations) and Greece (1 population) have been investigated. In all of them the basic number of 9 was established, but the degree of polyploidy varied. Plants from Austria and Czechoslovakia were diploid ( $2n=18$ ), from Hungary and Roumania tetraploid ( $2n=36$ ) and from Greece hexaploid ( $2n=54$ ) (Fig. 12). These observations agree with previous reports, in that the diploid number has only been reported from the western part of the area of distribution (Pólya 1947, 1948: Hungary; Kawaragi & Ohno 1964: Austria, Hungary and Roumania), and the tetraploid number from the eastern part (Tataryevski 1948: Roumania; Kawaragi & Ohno 1964: Hungary, Roumania, Bulgaria and the USSR). The hexaploid number has been reported before only in a study by Mitsuoka (1961) on "*Mibu-yomogi*, *Artemisia maritima* L. sep. *monophylla* Waldst. & Kit.", a source of santonin in Japan. I am not sure of the correctness of the taxonomic determination in this work.

Only one case of aneuploidy was recorded in the present investigation. A plant from the Cluj area in Roumania had 39 chromosomes (Fig. 12 E), as compared with 36 in other plants from the same area. No disturbances in root-tip mitosis have been observed.

### Meiosis and Pollen Viability

Male meiosis was studied in only a restricted number of diploid and tetraploid plants.

The number of PMCs analysable at metaphase I was small. Apparently only bivalents were formed in diploids, whereas cases of univalent



and multivalent formation were observed in tetraploids. Some disturbances were also noted in later stages, in both diploids and tetraploids, mostly in the form of bridges and laggards, some at anaphase I but most of them at anaphase II. The disturbances could be seen in most plants, but the total number of disturbed divisions was less than one per cent in the diploids, somewhat more in the tetraploids.

As a result of irregular meiosis several cases of abnormal tetrads were to be seen. The tetrad cells often differed in size and sometimes one or two extra nuclei, micronuclei, were observed. Two plants with giant pollen cells could be noted, both of them tetraploids from Roumania.

Not unexpectedly, pollen stainability values were rather low in many plants. Reduction in pollen fertility was apparent especially in tetraploids and hexaploids (Fig. 13) in which frequencies of 60--70 % stainable pollen grains were common. In one hexaploid plant a frequency of only 34 % was noted. Even if meiosis was not investigated in the hexaploids it can be presumed that meiotic irregularities are frequent, as pollen grains varying greatly in size could be observed in some of the plants. Thus, there were many micro- and, in one case, giant pollen grains.

In both diploids, tetraploids and hexaploids of A. santonicum vegetative propagation is fairly pronounced though not as extensive as in A. maritima. Judging from this and from the degree of meiotic aberration found, A. santonicum can probably be considered to be intermediate between A. maritima and A. vallesiaca as regards the inherent balance between reproduction by sexual and asexual means in each species.

### Chromosome Morphology

The absolute length of the somatic chromosomes varies with the fixative used between 2--3 and 4--5  $\mu$ . Most of them have submedian or nearly median centromeres. Chromosomes that are more asymmetric are also present at all ploidy levels. In diploids from Austria two pairs of chromosomes were of this type with more or less subterminal centromeres while plants from Czechoslovakia had three pairs of dis-

tinctly asymmetric chromosomes. Tetraploid plants from Hungary and Roumania had at least six pairs of chromosomes that could be seen to be distinctly asymmetric in most preparations, hexaploids from Greece at least nine. On the whole it seems that there is a tendency towards a more asymmetric karyotype in A. santonicum than in the species previously discussed.

The short arms of the asymmetric chromosomes have often secondary constrictions but the number and size of the satellites vary throughout the material. One third of the diploid plants had four satellites, the rest had two. From Czechoslovakia only plants with chromosome sets containing two satellite chromosomes have been observed.

In tetraploids two, four or six satellites were usually noted, located on the short arm of chromosomes with subterminal centromeres. Some plants from Hungary had a fourth pair of satellite chromosomes, but in this case the secondary constriction was located on the long arm of a rather asymmetric chromosome. In one of these plants heterozygosity for another secondary constriction was observed (Fig. 14 D, third pair), viz. one that cut off about two thirds of the long arm of a submetacentric chromosome. The constriction was very distinct and could be seen in all preparations made from this plant.

From the hexaploids no squash preparations were analysable, so nothing can be said with certainty about the number of satellite chromosomes present in these plants.

As regards the number of genomes probably combined in the polyploids there is no really conclusive evidence, except that some chromosome types in the tetraploids seem to be represented by single pairs only, e.g., in Fig. 14 D, pair no. 9 and pair no. 15. It is therefore probable that tetraploid A. santonicum is at least not an autopolyploid, provided that no gross rearrangements have taken place. The same deduction can be made from the results of the meiotic studies. Reservations for such an interpretation, as discussed previously, must be borne in mind, however.



# PHENOLOGY AND MORPHOLOGIC VARIATION

## MORPHOLOGIC CHARACTERS OF TAXA COMPARED

Morphological variation within each of the taxa has been analysed and compared. The primary values have been grouped in classes in tables and then treated statistically. Mean value (m) and standard deviation (s) are given for each character measured. In the diagrams all frequencies are given as percentages, and the mean values have been plotted (short vertical lines). Quantitatively varying characters are illustrated by the means of frequency polygons, the remainder as histograms.

The following numbers of flowering plants cultivated under uniform conditions have been analysed (see appendix for localities):

|                          |                                      |
|--------------------------|--------------------------------------|
| <u>Lotus maritima</u>    | 536 plants from 114 populations      |
| <u>Lotus vallesiacus</u> | 203 plants from 14 populations       |
| <u>Lotus santonicum</u>  | 88 plants from 12 populations,       |
| including                | 56 diploid plants (8 populations)    |
|                          | 24 tetraploid plants (3 populations) |
|                          | 8 hexaploid plants (1 population)    |

In L. santonicum most of the material consists of diploid plants. If all ploidy levels had been equally represented there would have been a shift to the right in some of the graphs illustrating absolute size, i.e., in cases where size is directly influenced by ploidy level. However, these cases are always discussed in the text and the mean values for each ploidy level are shown in the graphs (2, 4 and 6, respectively). In a following section detailed information on variation within each ploidy level will be given.

## VEGETATIVE DEVELOPMENT

All species are perennial. The aerial parts usually wither in the very late autumn, and renewal of growth takes place from buds on a rhizome. Under favourable conditions the stems do not wither completely but the lower parts survive and supply buds for renewal the following spring.

In A. maritima, and sometimes also in A. santonicum, plants in cultivation have been observed to produce adventitious buds from roots which thus function in the same way as rhizomes in the extension of the clone.

### Rhizomes

The young plant usually remains more or less acaulescent during the first year, bearing only a rosette of leaves. Fertile shoots are not produced until the second year at the earliest. Nor does the rhizome develop fully until the second vegetative period. A. maritima, A. vallesiaca and A. santonicum all display more or less vigorous propagation from the often well-developed rhizome which is lignified and branched to a varying degree in all species. Most of the buds on the rhizome produce only rosette-bearing shoots, and this is the rule for newly-developed parts of the rhizome. During the second vegetative period of a section of the rhizome and later, one or a few buds produce fertile shoots. Several rhizome internodes are usually developed each year. The nodes of the rhizome bear triangular, scale-like leaves.

A. maritima readily forms large clones, frequently up to 5 m in diameter, owing to the rapid growth of the often more or less stoloniferous rhizomes, several internodes, 10--30 mm long, being produced each year. The oblique to horizontal rhizomes are mostly smooth in appearance, 3--8 mm in diameter and moderately branched. Lignification is usually moderate, though there are examples of ecotypes with very thick woody rhizomes, e.g. the Bohuslän ecotype (western Sweden). In sandy biotopes the internodes at times are very short so that the plants form tufts. Such plants have been observed for instance on some sandy shores of western Jylland (Denmark).

A. vallesiaca. The rhizome is sturdy (c. 5--10 mm in diameter),



strongly lignified and presumably lives for a great many years so that the plant may become very old. The surface is rough and fibrous. A large number of fertile as well as sterile rosette-bearing shoots are produced each year. As the rhizome internodes are much shorter than in the other species (1--7/--10 mm) and the branching is rich, the plants will attain a tufted appearance. A clone will cover a much smaller area than those of A. maritima, for instance, that is vegetative propagation is less pronounced, but this is compensated for by the greater length of life of each plant. The rhizomes are often strongly ascendant but in most cases wholly subterranean.

A. santonicum. The weakly to moderately branched rhizome has a fairly smooth surface and is often reddish in colour. The internodes are about 1--3 mm in diameter and 5--10(--20) mm long in diploids, c. 3--5 mm and 10--15 mm, respectively, in polyploids. Moderately rapid growth each year will produce clones usually covering one to a few square metres. The rhizome is horizontal--slightly ascending, sometimes growing above the substrate. Vegetative propagation is reduced in arid biotopes, and at all events is not so effective as in A. maritima.

### Stems

All observations have been made on fertile shoots.

Shoot length. There is great variation in shoot length in all species (Fig. 15). The tallest individuals are found in A. vallesiaca, but this species also has the highest dispersion value. Extremely short individuals are found only in A. maritima, and these mainly belong to a certain form series (or ecotype) on Öland and Gotland. Another form series (in Bohuslän, Sweden) represents most of the taller individuals in this species.

|                         | m   | s    |                            |
|-------------------------|-----|------|----------------------------|
| <u>A. maritima</u>      | 320 | +95  |                            |
| <u>A. vallesiaca</u>    | 533 | +139 |                            |
| <u>A. santonicum</u> 2x | 448 | +76  | Measurements in mm (+1 mm) |
| 4x                      | 480 | +122 |                            |
| 6x                      | 445 |      |                            |

It is interesting to note that while in A. maritima the average shoot length is about the same in cultivated plants as in nature (though showing a slight increase), A. vallesiacae and A. santonicum are undoubtedly favoured by conditions of cultivation, as shown by the marked increase in growth in most individuals of these species. In the latter species the differences between the three ploidy levels are small in cultivation, even smaller than in nature. In cultivation as well as in nature, however, the tallest individuals are to be found among the tetraploids.

Suffrutescence. The material is divided into three groups as follows:

- 1 Slightly suffrutescent; thin, easily flexible stems
- 2 Moderately suffrutescent; rather rigid stems
- 3 Strongly suffrutescent; sturdy, inflexible stems

There are of course no definite distinctions between the groups. Where there has been any doubts plants have probably mostly been placed in group 2, which may thus be somewhat over-represented.

The stems are mostly woody at the base only, though in group 3 the greater part of the stem is lignified.

A. maritima and A. santonicum are usually moderately suffrutescent (Fig. 16 A), but in addition a rather large group of thin-stemmed individuals is found in A. maritima. As will be seen (section on intra-specific variation), this group largely represents the ecotype on Öland and Gotland.

A. vallesiacae is distinguished by its high degree of suffrutescence (cf. the thick woody rhizomes of this species). More than half of the material has been placed in group 3, the rest in group 2. The strong lignification is accompanied by a greater hardness, and normally the stems do not wither completely during the winter. Buds on the lower parts of the stems develop into new shoots the following spring, together with shoots from the rhizome.

Pubescence. The material is divided into four groups as follows:

- 1 Almost glabrous
- 2 Moderately pubescent, greyish-green (sometimes tinged with red or yellow)
- 3 Densely pubescent, grey
- 4 Very densely pubescent, almost white

There is a striking difference in pubescence between A. vallesiacae and A. santonicum (Fig. 16 B) in that A. vallesiacae is dense-



ly covered with a white or greyish-white mat of hairs, A. santonicum is usually almost glabrous, particularly the diploids and tetraploids. In A. maritima all types of pubescence are represented, a form series often being characterized by the degree of pubescence. However, most maritima forms by far are greyish in colour, i.e., they are rather densely pubescent.

In nature most forms are more densely pubescent. Even A. santonicum may be greyish in colour but there is a gradual decrease in pubescence as the plants mature.

In all cases the indumentum comprises 10-celled glands, which will be described later, and T-shaped hairs of the same type as described by Mülloffer (1933) for A. caerulea (belonging to the A. maritima complex), and by Diettmer (1938) for A. tridentata, a North American species of the subgenus Seriphidium in the traditional sense. Each hair consists of an apical cell, c. 10--20  $\mu$  in diameter, medifixed on a stalk of two to three cells (Fig. 17). The hairs are usually very long, each arm measuring between 300 and 600  $\mu$ . There is no great difference in size of hairs in the three species, except that in diploid A. santonicum hairs are generally somewhat smaller (Fig. 17 D). Extremely coarse hairs, 1500  $\mu$  long and more than 20  $\mu$  in diameter, have occasionally been observed especially in A. maritima and A. vallesiaca.

The apical cell dies soon after the hair matures, but the stalk cells usually remain alive for a long time. The thin-walled empty apical cells are responsible for the white or greyish colour of the indumentum.

## Leaves

The first pair of leaves to develop after the cotyledons are opposite and oblanceolate in shape with entire margins (Figs. 87 B, E, H, 88 C). All leaves that subsequently appear are alternate and more or less dissected.

The "rosulate" leaves of the sterile shoots and the lower cauline leaves are of the same general type: usually 2--3(--4)-pinna-tisect with linear or somewhat spatulate segments. Auricles of

varying size are often present, in A. vallesiaca practically always. The auricles may be small and entire (Figs. 18 I, J, 19 G) or large and pinnatisect (Figs. 18 A, E, M, 19 A, E), the transition from leaf segments to auricles sometimes being gradual, in which case the leaves appear to be almost sessile, a common condition in A. vallesiaca.

The structure of the leaves changes successively towards the apex of the stem and particularly on the branches. The number of segments decreases gradually and in many plants the upper synflorescence leaves are undivided and linear, more or less bract-like (Figs. 18 I, M--O, 19 G). The same variation in structure occurs in all three species, though the simple bract-like type is rare in A. vallesiaca, where the leaves are often extensively dissected throughout the synflorescence and apparently sessile, almost amplexicaul (especially in the Italian populations). On the other hand bract-like upper leaves are very frequent in A. santonicum, particularly in the diploids where they are often extremely small and narrow.

The following observations are all based on leaves one third of the way up the stem. Two leaves on each plant have been studied.

Size and shape. The length of the lamina has been measured (Fig. 20). In the case of almost sessile leaves the values noted will correspond to practically the whole leaf length.

|                      |    | m    | s    |                               |
|----------------------|----|------|------|-------------------------------|
| <u>A. maritima</u>   |    | 23.8 | +9.3 |                               |
| <u>A. vallesiaca</u> |    | 17.3 | +6.6 |                               |
| <u>A. santonicum</u> | 2x | 15.8 | +4.8 | Measurements in mm<br>(+1 mm) |
|                      | 4x | 24.5 | +6.8 |                               |
|                      | 6x | 39.0 |      |                               |

Variation is great in all species. In A. santonicum the differences between the three ploidy levels are often distinct, however. The leaves in diploids are generally very small, particularly in Czechoslovakian plants (Fig. 19 H).

As seen by the mean values, A. maritima generally has longer leaves than A. vallesiaca. The difference would appear even greater if the Öland/Gotland form series was left out of consideration, as most of the small-leaved individuals belong to this series. Two peaks in the maritima graph indicate the existence of two form series.

As a measure of the breadth of the lamina the length of the



longest primary segment (usually situated slightly below the middle of the lamina) was noted. But as variation in absolute breadth is not independent of length variation, these figures are not given. Instead, the lamina length/primary segment length ratio has been calculated. The magnitude of this ratio is indicative of the narrowness of the leaf (Fig. 21).

|                         | m    | s     |
|-------------------------|------|-------|
| <u>A. maritima</u>      | 2.18 | +0.39 |
| <u>A. vallesiaca</u>    | 2.45 | +0.60 |
| <u>A. santonicum</u> 2x | 2.10 | +0.34 |
| 4x                      | 2.28 | +0.35 |
| 6x                      | 2.60 |       |

It is evident that the leaves of A. vallesiaca in general are more elongate than in the other taxa, hexaploid A. santonicum excepted. The variation is extensive in all species, however, especially in A. vallesiaca.

Segmentation. As a measure of the degree of leaf segmentation the ratio of the number of segments on the longest primary segment to the length of this primary segment has been calculated. A high value implies that the leaf is much dissected (Fig. 22).

|                         | m    | s     |
|-------------------------|------|-------|
| <u>A. maritima</u>      | 0.62 | +0.31 |
| <u>A. vallesiaca</u>    | 1.67 | +0.69 |
| <u>A. santonicum</u> 2x | 0.83 | +0.27 |
| 4x                      | 0.63 | +0.22 |
| 6x                      | 0.60 |       |

In this respect, too, A. vallesiaca differs from the other species. The vallesiaca leaf is often as much as 3--4-pinnatisect, with crowded and entangled segments. A. maritima and A. santonicum have generally 2--3-pinnatisect leaves.

Size and shape of the segments. The length and breadth of the secondary segments on the longest primary segment have been measured and plotted in a scatter diagram (Fig. 23). From such a diagram it is possible to estimate the variation in size as well as in shape.

|                      |    | Breadth |       | Length |      |
|----------------------|----|---------|-------|--------|------|
|                      |    | m       | s     | m      | s    |
| <u>A. maritima</u>   |    | 0.65    | +0.15 | 6.6    | +3.2 |
| <u>A. vallesiaca</u> |    | 0.42    | +0.06 | 4.8    | +1.6 |
| <u>A. santonicum</u> | 2x | 0.47    | +0.09 | 4.4    | +1.5 |
|                      | 4x | 0.67    | +0.13 | 5.5    | +1.8 |
|                      | 6x | 0.70    |       | 5.3    |      |

Measurements in mm  
(breadth +0.05 mm,  
length +0.1 mm)

It is evident that variation in size and shape is approximately the same in A. vallesiaca and diploid A. santonicum, though there is a slight tendency in the latter to have broader segments. In tetraploid and hexaploid A. santonicum the segments are much alike, generally broader and less elongate than in the diploids. The mean values are rather close to those of A. maritima, but in the latter species variation is extensive. It is possible to find forms with small and narrow segments, like those of A. vallesiaca, as well as forms with short and very broad, or long and narrow segments etc. However, the segments are generally longer and broader in A. maritima than in the other two species.

The ultimate leaf segments in A. vallesiaca and A. santonicum are usually linear with a pointed or seldom blunt apex (Fig. 24). Sometimes (especially on sterile shoots) slightly spatulate segments are to be found. In A. maritima such segments are very common. In this species the apices are generally subacute, but forms with blunter segments are frequently met with, particularly in some Swedish form series (Fig. 25).

Pubescence. The material has been classified into the same four groups as for stem pubescence (p.29).

The variation pattern of leaf pubescence is not unexpectedly the same as for stems, except that there is a slight shift towards a higher degree of pubescence (Fig. 26). That is, A. santonicum is sparsely pubescent with greyish-green leaves while A. vallesiaca is covered with a dense mat of white hairs. The maritima leaves are mostly greyish, though some form series are characterized by a sparse, some by a dense pubescence.

Stomata. Stomata are found scattered (c. 80--100 per sq.mm) on both sides of the leaf. No particular difference in size, shape or distribution on abaxial and adaxial sides has been noted. Along the midrib and the leaf margins, however, the stomata are usually longer.

The number of stomata per square unit is somewhat higher in diploid A. santonicum than in the other taxa. This may be due to the



general difference in cell size, which is a consequence of the different ploidy levels, diploids having smaller cells.

The stomatal length has been defined as the length of the guard cells. Measurements were made on dried material softened by boiling (N.B. cultivated material only, as stomatal size is to some degree influenced by external factors). Preparations were made from 2--3 well-developed leaves on the lower third of the stem. 20 stomata were measured in each preparation.

|                         | m    | s           |                                                         |
|-------------------------|------|-------------|---------------------------------------------------------|
| <u>A. maritima</u>      | 32.6 | <u>+2.9</u> |                                                         |
| <u>A. vallesiaca</u>    | 28.1 | <u>+2.0</u> |                                                         |
| <u>A. santonicum</u> 2x | 22.6 | <u>+2.1</u> | Measurements in $\mu$ ( <u><math>\pm 1 \mu</math></u> ) |
| 4x                      | 32.6 | <u>+3.5</u> |                                                         |
| 6x                      | 31.5 |             |                                                         |

The difference in mean value between diploid A. santonicum and the rest of the material is statistically highly significant (Fig. 27). Variation and mean value are approximately the same in polyploid A. santonicum and A. maritima while A. vallesiaca is intermediate between these and the diploids. This implies that stomatal length is of some diagnostic value, at least in estimating the ploidy level as diploids can be fairly easily separated from polyploids.

The overlapping seen in graphs for cultivated material of A. maritima and A. vallesiaca, for instance, is less pronounced in material grown under natural conditions as was shown by an investigation. Stomata in herbarium specimens and specimens collected and pressed by the author were measured and the values plotted in graphs with the values of the cultivated material. In A. vallesiaca the mean values proved to be almost identical. In A. maritima, however, there was a pronounced shift to the right in the graph of the spontaneous material as compared to the cultivated material (Fig. 28).

Synflorescence

The flowering shoot system is a synflorescence with lateral capitulous branches of varying order arranged in a racemose fashion. The capitula-bearing peduncles are in most forms of all three species of a secondary or tertiary order, very seldom more complicated. Very simple synflorescences are found in some form series of A. maritima (e.g. the Öland/Gotland ecotype). Some are almost spicate, in others short branches of a primary order support single terminal (pseudoterminal) heads.

Note: there is a marked increase in branching in cultivated plants as compared with plants grown under natural conditions, especially in A. vallesiaca.

Symmetry. The material was classified into four groups.

- 1 Wholly secund synflorescence
- 2 Largely secund synflorescence
- 3 Slightly secund synflorescence
- 4 Branches diverging in all directions

There is some variation in synflorescence symmetry in all species (the asymmetry of course being false, as the branches are merely bent over from one side to the other). Wholly secund branching systems are found in A. santonicum, chiefly in hexaploids, and in A. maritima. The latter species also varies most. In most forms of A. santonicum (above all diploids and tetraploids) and, in particular, A. vallesiaca the branches diverge in all directions or only slightly unilaterally (Fig. 29 A).

Length of synflorescence. The length of the synflorescence has been measured and the values obtained plotted against the corresponding shoot length values in a scatter diagram (Fig. 30).

|                      | Synflorescence |      | Shoot |      |      |
|----------------------|----------------|------|-------|------|------|
|                      | m              | s    | m     | s    |      |
| <u>A. maritima</u>   | 167            | +82  | 320   | +95  |      |
| <u>A. vallesiaca</u> | 323            | +133 | 533   | +139 |      |
| <u>A. santonicum</u> | 2x             | 278  | +73   | 448  | +76  |
|                      | 4x             | 303  | +97   | 480  | +122 |
|                      | 6x             | 235  |       | 445  |      |

Measurements in mm  
(+1 mm)



Variation in the length of the synflorescence fairly closely follows shoot length variation. In the diploids and tetraploids the ratio of synflorescence length to shoot length is about 0.6. The same ratio in hexaploids is usually only about 0.5, that is, the synflorescence is generally shorter in relation to shoot length. The most pronounced variation in the ratio of the two length values is seen in A. vallesiaca, as shown by the greater vertical distance between any two limits in the diagram.

The branches. Branch length varies to a great extent in all species. Nor does the length of a particular branch seem to be correlated with its position on the stem (except the upper branches), the longest branches sometimes being found in the middle of the synflorescence, sometimes at the base. However, the lower branches are usually rather short bearing few or no capitula.

A morphological character often used for the delimitation of taxa in the A. maritima complex is degree of rigidity of the branches (erect--pendent). The author's investigation has shown that except for A. vallesiaca the variation is too extensive for branch rigidity to be of any diagnostic value.

The material investigated was divided into three groups as follows:

- 1 Branches wholly pendent
- 2 Terminal parts of branches drooping
- 3 Branches erect

In A. vallesiaca branches are nearly always erect (Fig. 29 B), and this is often so in diploid A. santonicum. In tetraploids and hexaploids in the latter species plants with branches wholly or partly recurved are in the majority though erect forms are also fairly common. The greatest variation is found in A. maritima. Plants of this species belonging to all three groups have been observed growing together in the same population. However, the branches are usually more or less pendent.

The branches are always leafy, the leaves varying from pinnatisect to linear and bract-like. The branches of the highest order bear the smallest and most bract-like leaves.

Number and position of the capitula. Using two primary branches in the middle of the synflorescence on each plant, length of branch (in mm) and number of capitula were investigated. The ratio of the two values (number of capitula/length of branch) was calculated and plotted in a graph (Fig. 31) to show the variation in capitulum

density.

|                      |    | m    | s          |
|----------------------|----|------|------------|
| <u>A. maritima</u>   |    | 0.42 | $\pm 0.21$ |
| <u>A. vallesiaca</u> |    | 0.26 | $\pm 0.15$ |
| <u>A. santonicum</u> | 2x | 0.45 | $\pm 0.19$ |
|                      | 4x | 0.58 | $\pm 0.18$ |
|                      | 6x | 0.58 |            |

Variation is great in all species, especially in A. maritima in which the most densely capitulous plants are found as well as forms with very long internodes and sparse capitula. An extreme coarctate type is occasionally observed in all species. The highest proportion of plants with densely placed capitula is found in A. santonicum, particularly in the polyploids. In this species as well as in A. maritima, however, there are normally 2--7 capitula per mm on the branches concerned, while there are usually only 1--4 per mm in A. vallesiaca.

As the position of the capitula on the branches is a "key" character this was also investigated.

The material was classified as follows:

- 1 Unilateral position of the capitula, these often pendent
- 2 Mixed condition, more like 1
- 3 Mixed condition, more like 4
- 4 Multilateral position of the capitula, these often erect

Note: the capitula are of course not borne unilaterally, they are merely bent over from one side of the branch to the other.

This character also proved to be of little value as a systematic character. Variation is too great. Only in A. vallesiaca can a fairly pronounced tendency be observed, viz., that the capitula are normally multilaterally placed and are more or less erect (Fig. 29 C).

Peduncle length. Whether the capitula are pendulous or erect depends to some extent on the length of the peduncles, e.g. long-stalked capitula are mostly pendulous.

The peduncles on a branch in the middle of the synflorescence were measured and the mean value for each branch plotted in a graph (Fig. 32).

|                      |    | m   | s         |                                       |
|----------------------|----|-----|-----------|---------------------------------------|
| <u>A. maritima</u>   |    | 0.7 | $\pm 0.5$ |                                       |
| <u>A. vallesiaca</u> |    | 0.4 | $\pm 0.5$ |                                       |
| <u>A. santonicum</u> | 2x | 1.1 | $\pm 0.9$ | Measurements in mm<br>( $\pm 0.1$ mm) |
|                      | 4x | 0.8 | $\pm 0.6$ |                                       |
|                      | 6x | 0.8 |           |                                       |



The dispersion values are very high in all cases. In A. santonicum especially there is great variation. It is evident, however, that A. vallesiaca generally has short-stalked capitula, often almost sessile, thus usually being erect.

## Capitula

Shape and size. The capitula are more or less ovoid in shape (Figs. 33, 34). The most rounded heads are found in A. maritima, the most oblong ones in A. santonicum, especially in diploids and some tetraploids. The width of the involucre is dependent on three factors: 1) how closely the phyllaries surround the florets; in A. santonicum the phyllaries surround the florets more closely than in the other species; 2) the size of the phyllaries; 3) the number of florets per head. Variation in size of capitula is greatest in A. maritima. In some form series very large heads are frequent, e.g. in Bohuslän (western Sweden) and parts of Great Britain (Fig. 33 C, K). On the other hand the ecotype on Öland and Gotland is distinguished by its unusually small capitula (Fig. 33 D, E). In A. santonicum the diploids generally have smaller heads than the polyploids.

Size and shape of the phyllaries. There is a gradual transition from ordinary leaves to phyllaries. The leaves gradually diminish in size and the transition forms are small and narrow. The outer phyllaries are very small with a gradual increase inwards first in breadth then in both breadth and length. The difference in size between outer and inner phyllaries is greatest in A. santonicum giving the involucre a distinctly imbricate appearance. The typical maritima capitula have somewhat spreading phyllaries slightly different in length. The vallesiaca involucre is more or less intermediate between those of the other two species.

The breadth of the inner phyllaries was measured and the mean values from ten measurements per plant were plotted in a graph (Fig. 35).

|                      |    | m   | s    |                                 |
|----------------------|----|-----|------|---------------------------------|
| <u>A. maritima</u>   |    | 1.6 | +0.3 |                                 |
| <u>A. vallesiaca</u> |    | 1.2 | +0.2 |                                 |
| <u>A. santonicum</u> | 2x | 1.2 | +0.2 | Measurements in mm<br>(+0.1 mm) |
|                      | 4x | 1.4 | +0.2 |                                 |
|                      | 6x | 1.5 |      |                                 |

The phyllaries are narrow in both A. vallesiaca and diploid A. santonicum, in the polyploids of the latter species usually somewhat broader (Fig. 36 R--X). In A. maritima the variation is pronounced (Fig. 36 A--Q). Forms with narrow phyllaries as well as forms with extremely broad ones have been observed. About 25 % of the maritima plants have phyllaries that are broader than any phyllaries observed in either A. santonicum or A. vallesiaca. The length of the phyllaries varies more or less with the breadth, but in some maritima forms the breadth/length ratio is markedly high (Fig. 36 D, F, M, O).

The outer phyllaries are usually narrowly to broadly triangular in all species, with a more or less blunt to subacute apex. In some forms, typically in A. vallesiaca, they are even distinctly mucronate (Fig. 34 C). The inner phyllaries are also mostly acute to subacute in A. vallesiaca and A. santonicum (at least in the diploids and many of the polyploids), more seldom in A. maritima. In this species the inner phyllaries are generally more or less blunt. In general outline the inner phyllaries are elliptic to obovate in all three species.

Phyllary margins. The margins of the phyllaries are increasingly scarious from the outer to the inner phyllaries. In the outer phyllaries the scarious margins are either very narrow for the whole of their length, or broad at the base and then abruptly narrowing towards the apex, the latter being typical for A. vallesiaca. The inner phyllaries are usually green and fleshy for only a narrow strip along the midrib. This herbaceous region is somewhat different in outline in the three species.

A. maritima: herbaceous midrib region mostly more or less spatulate with a subacute to obtuse apex (e.g. Fig. 36 D--Q).

A. vallesiaca: herbaceous midrib region linear or slightly spatulate with a subacute (seldom blunt) apex (e.g. Fig. 36 R--T).

A. santonicum: herbaceous midrib region tapering towards the apex (e.g. Fig. 36 U, W) or more or less linear (e.g. Fig.



36 V, X) with an acute to subacute (seldom blunt) apex.

Sometimes the inner part of the membranous margins is tinged with red (frequently in A. santonicum). The margins may also be ciliate, at least in the apical part, with scattered very long hyaline hairs (Fig. 36 B, L, N, S).

The breadth of the scarious margins of the inner phyllaries was measured at the broadest part (Fig. 37).

|                      |    | m    | s     |                                  |
|----------------------|----|------|-------|----------------------------------|
| <u>A. maritima</u>   |    | 0.56 | +0.13 |                                  |
| <u>A. vallesiaca</u> |    | 0.36 | +0.10 |                                  |
| <u>A. santonicum</u> | 2x | 0.39 | +0.10 | Measurements in mm<br>(+0.05 mm) |
|                      | 4x | 0.48 | +0.10 |                                  |
|                      | 6x | 0.50 |       |                                  |

The breadth of the margins varies with the variation in phyllary breadth except that the ratio of phyllary breadth to margin breadth is slightly higher in A. vallesiaca than in the other two species, that is the phyllaries of A. vallesiaca generally have the narrowest margins both actually and proportionate to phyllary breadth.

Vestiture. The herbaceous parts of the phyllaries are generally glandular-pubescent. There is a gradual decrease in pubescence from the outer to the inner phyllaries. The latter are often glandular-pubescent in the upper half only. The hairs are T-shaped as on stems and leaves. Most of them are rather short and woolly, but some are extremely long and coarse.

The degree of pubescence in the different species complies to the same pattern as that of the stems and leaves (Fig. 38). A. santonicum has sparsely pubescent outer phyllaries while the inner phyllaries are practically glabrous (except for a few glands). The phyllaries of A. vallesiaca are densely pubescent, the inner ones at least in the upper half. In A. maritima there is a great variation from sparsely to densely pubescent phyllaries, the degree of pubescence often being characteristic of a given ecotype.

Number of florets (Fig. 39). In diploid A. santonicum each capitulum usually contains 2--4 florets (Fig. 40 G), sometimes only one. The tetraploids often have double the number (Fig. 40 H). In the other species there is greater variation, about 3--8 being the usual number (Fig. 40 B, D). Greater numbers are found especially in A. maritima, either in forms with large involucres (Fig. 40 A, C) or in coarctate forms.

|                      |    | m   | s           |                                        |
|----------------------|----|-----|-------------|----------------------------------------|
| <u>A. maritima</u>   |    | 6.2 | <u>+2.5</u> |                                        |
| <u>A. vallesiaca</u> |    | 5.3 | <u>+1.5</u> |                                        |
| <u>A. santonicum</u> | 2x | 3.3 | <u>+1.1</u> | Ten capitula per plant<br>were counted |
|                      | 4x | 4.1 | <u>+1.0</u> |                                        |
|                      | 6x | 3.8 |             |                                        |

Receptacle. There are neither hairs nor bracts at the base of the florets on the inside of the receptacle. A glabrous receptacle is characteristic of the whole subgenus Seriphidium.

### Floret

Sex of florets. When Waldstein & Kitaibel (1802 p. 77) described the Hungarian species later to be recognized as Artemisia santonicum L., they named it A. monogyna owing to the alleged existence in each capitulum of one pistillate flower together with the ordinary bisexual ones. This condition would resemble the arrangement found in other subgenera of Artemisia of a group of hermaphrodite florets surrounded by more or less zygomorphic pistillate florets ("ray" florets). Śagórski (1907, 1908) interpreted the name monogyna as referring to the existence of so-called "gynodynamic" flowers in the species. Śagórski described such flowers as having the pistil protruding from the corolla tube, while in other flowers the pistil was wholly surrounded by the corolla with the stigmas below the level of the corolla mouth.

The present author's investigation has shown that in all species, including A. santonicum, all florets in the capitulum are hermaphrodite and actinomorphic (see capitula sections Fig. 40). The position of the stigmas in the corolla tube varies sometimes from floret to floret or usually from plant to plant in all species, though protruding pistils are more frequent in A. maritima than in the other two species. Sometimes (as a rule in many-flowered capitula) one or a few florets in a head do not mature, probably as a result of lack of space and nutrition. But initials for both sexes are present as seen in cross-sections. This together with the fact that it often



happens that only one of the few florets in each head is fertilized can perhaps explain the misleading name monogyna.

Shape and size of corolla. All florets in a head are alike in appearance, having a tubular five-lobed corolla (Fig. 44), five syn-  
genesious stamens, a pistil with a two-branched style and an infe-  
rior ovary. Pappus is missing.

The length of the corolla tube was measured using ten samples from each plant (Fig. 41).

|                      |    | m    | s          |                                       |
|----------------------|----|------|------------|---------------------------------------|
| <u>A. maritima</u>   |    | 2.84 | $\pm 0.23$ |                                       |
| <u>A. vallesiaca</u> |    | 2.81 | $\pm 0.22$ |                                       |
| <u>A. santonicum</u> | 2x | 2.29 | $\pm 0.12$ | Measurements in mm<br>( $\pm 0.1$ mm) |
|                      | 4x | 2.52 | $\pm 0.17$ |                                       |
|                      | 6x | 2.40 |            |                                       |

In A. maritima and A. vallesiaca similar variation in corolla length was found, the mean value and dispersion value being almost identical. The corolla is usually about 2.5--3 mm long in these species. On the whole the florets of A. santonicum are somewhat smaller, even in the polyploids, the corollas of which are gene-  
rally about 2.3--2.7 mm long. In the diploids the corollas are even shorter, c. 2.2--2.4 mm, and as a rule also narrower.

The length (varying between 0.3 and 0.6 mm) and breadth (0.3--0.5 mm) of the corolla lobes were also noted in each case, and variation in lobe shape was calculated from the ratio of the two values measured (Fig. 42). Since there is some variation in the extension of the incisions in the corolla, the length of corolla/length of corolla lobe ratio was also calculated (Fig. 43).

| Length/breadth of corolla lobe |    |      |            | Corolla length/corolla lobe length |    |      |            |
|--------------------------------|----|------|------------|------------------------------------|----|------|------------|
|                                |    | m    | s          |                                    |    | m    | s          |
| <u>A. maritima</u>             |    | 1.12 | $\pm 0.11$ | <u>A. maritima</u>                 |    | 6.54 | $\pm 0.65$ |
| <u>A. vallesiaca</u>           |    | 1.40 | $\pm 0.15$ | <u>A. vallesiaca</u>               |    | 5.69 | $\pm 0.62$ |
| <u>A. santonicum</u>           | 2x | 1.28 | $\pm 0.11$ | <u>A. santonicum</u>               | 2x | 5.34 | $\pm 0.41$ |
|                                | 4x | 1.23 | $\pm 0.12$ |                                    | 4x | 6.00 | $\pm 0.53$ |
|                                | 6x | 1.21 |            |                                    | 6x | 5.35 |            |

In A. maritima corolla lobes are frequently more broadly triangular than in the other species, and this is especially pronounced in some form series (Halland--Bohuslän, Öland--Gotland; Fig. 44 B--D). In both A. vallesiaca and A. santonicum corolla lobes are more or less lanceolate, most distinctly so in many vallesiaca individuals. The

same type may also be found in A. maritima in some of the marsh populations (Fig. 44 A, E, F).

The part of the corolla that is incised is smallest in A. maritima, largest in diploid and hexaploid A. santonicum. In the latter species corolla incisions are relatively shorter in tetraploids than in the other ploidy levels. The length of the corolla lobes is about the same in tetraploids and hexaploids, but corollas are generally somewhat longer in the former.

Colour. The colour of the corolla varies in all species from pale yellow to deep red. There is no correlation with size and shape of corolla or inflorescence. Individuals in the same population may be of any colour. Pure yellow corollas are rare, however, especially in diploid A. santonicum. Often the part of the corolla to which the filaments of the stamens adhere is of a different shade, mostly greenish so that the corolla tube is distinctly divided into two portions.

Vestiture. The corolla is devoid of trichomes, but glands are scattered all over the surface and are densest on the basal part of the corolla and on the lobes. The type and distribution of glands will be discussed in the next section.

Periodicity. The three species are all anemophilous and cross-pollinating. Isolation of inflorescences has shown that the plants are completely self-sterile in all taxa.

The flowers are protandrous with the mechanism typical for Asteraceae: the thecae dehisce introrsely and the pollen is shed into the tube formed by the anthers and pushed into the corolla mouth by the fast-growing pistil, which takes only a few hours.

Thirty plants of each species (representing 11 populations of A. maritima, 7 of A. vallesiaca and 8 of diploid A. santonicum) were observed as regards the duration of each phase of flowering after the onset of anthesis (interpreted as the moment the pollen reaches the corolla mouth and is spread).

- 1) Time from anthesis to recurving of stigmatic branches (Fig. 45)
- 2) Time from recurving to withering of stigmatic branches (Fig. 45)
- 3) Duration of flowering  $(1) + 2)$  / per head (Fig. 46)
- 4) Duration of flowering per plant (Fig. 46)

3) and 4) are naturally dependent on the number of florets per head and the number of heads per plant, respectively.

It will be seen that the period from the onset of anthesis till



the recurving of the stigmatic branches is very short in A. vallesiaca (6--24 hours), noticeably longer in A. maritima and A. santonicum. The stigmas, however, persist much longer in A. vallesiaca than in the other species (4--6 days in A. vallesiaca, 1--3 days in A. maritima and 1--2 days in A. santonicum), which explains the values for 3) and 4). A. vallesiaca and A. maritima have about the same number of florets per head, and the sequence of anthesis of the different florets in a head is about the same, but as the total time of flowering  $(1) + 2)$  is longer in A. vallesiaca, this will also be true for the whole capitulum. The same applies to the plant taken as a whole in these two species.

The total time of flowering per floret is short in Artemisia santonicum. Although the synflorescence often comprises as many as 500--700 heads (A. maritima and A. vallesiaca 50--300), the total flowering period for the plant is frequently shorter than in the other species, as in A. santonicum the heads in a synflorescence flower almost simultaneously, which is not the case in A. maritima and A. vallesiaca.

These observations were made on cultivated material. Roughly the same course of events will be found in nature. A short flowering period is often characteristic of plants living in extreme conditions. This is true of A. santonicum: at the time of flowering the soils of the often highly saline biotopes are frequently dry and very hard, a result of the aridity of the climate in the areas concerned.

The flowering period occurs at somewhat different times of the year for the three species, both in cultivation and in nature. In addition intra-specific variation has been noted in A. maritima (Table 6).

### Glands

Glands are found scattered on stems, leaves, phyllaries and corolla tubes. They are of the same general type in all species. Each gland consists of two rows of secreting cells, generally four cells in each row, and two basal cells. In mature glands the horizontal

cell walls more or less degenerate and the cell contents are secreted. The degenerated glands have a sac-like appearance.

The species differ only slightly in size and shape, especially A. santonicum as compared with A. maritima and A. vallesiaca (Fig. 47). Thus the glands of at least the diploid and tetraploid forms of A. santonicum are usually more rounded, and moreover, in the diploids they are distinctly smaller than in the rest of the material investigated.

The density of the glands varies on different organs. On the leaves there are about 1--10 glands per square mm, on the corolla tubes about 1--20 per sq. mm.

The absolute number of glands per floret was counted (five samples from each individual) (Fig. 48). The mean value is lowest in the diploids, as would be expected from the smaller size of the corolla. But real differences in gland density are also apparent in the material. Thus polyploid A. santonicum generally has smaller florets than the other two species, but the number of glands is greater, especially in the hexaploids. A. maritima and A. vallesiaca also differ slightly in gland density, as the former has a greater number of glands on a corolla of about the same size as that of the latter. However, there is great variation within each species, in A. maritima from a few to 130 glands per floret.

|                      |    | m  | s   |
|----------------------|----|----|-----|
| <u>A. maritima</u>   |    | 54 | +21 |
| <u>A. vallesiaca</u> |    | 42 | +18 |
| <u>A. santonicum</u> | 2x | 31 | +14 |
|                      | 4x | 58 | +17 |
|                      | 6x | 80 |     |

### Stamens

As in other Asteraceae the stamens are syngenesious (according to Fernald, 1961 p. 105 the anthers are coherent, not connate, the latter implying a more intimate union of similar structures). The anthers are basifixed and the filaments are adnate to the corolla tube in the lower parts. The connective between the anther-sacs



is distally provided with a lanceolate appendage. Also the anthers are appendaged with basal tail-like projections. Dehiscence is introrse.

The length of the thecae was measured (Fig. 49).

|                      |    | m    | s          |                                       |
|----------------------|----|------|------------|---------------------------------------|
| <u>A. maritima</u>   |    | 1.11 | $\pm 0.14$ |                                       |
| <u>A. vallesiaca</u> |    | 1.15 | $\pm 0.15$ |                                       |
| <u>A. santonicum</u> | 2x | 0.95 | $\pm 0.10$ | Measurements in mm<br>( $\pm 0.1$ mm) |
|                      | 4x | 1.10 | $\pm 0.08$ |                                       |
|                      | 6x | 1.06 |            |                                       |

The thecae are long and narrow in A. vallesiaca, relatively thicker in the other species and also shorter in some cases (some maritima form series and, especially, diploid A. santonicum; Fig. 50).

The length of the connective appendage was also measured (Fig. 51).

|                      |    | m    | s          |                                        |
|----------------------|----|------|------------|----------------------------------------|
| <u>A. maritima</u>   |    | 0.34 | $\pm 0.04$ |                                        |
| <u>A. vallesiaca</u> |    | 0.32 | $\pm 0.03$ |                                        |
| <u>A. santonicum</u> | 2x | 0.28 | $\pm 0.03$ | Measurements in mm<br>( $\pm 0.05$ mm) |
|                      | 4x | 0.31 | $\pm 0.02$ |                                        |
|                      | 6x | 0.32 |            |                                        |

The mean values are very similar, the length usually varying between 0.30 and 0.35 mm except in diploid A. santonicum in which appendages generally measure only 0.25--0.30 mm. In A. maritima there are forms in which the appendage exceeds 0.40 mm.

Some differences in appendage shape have been observed. Thus the appendages are practically always acute and narrow in A. vallesiaca, but frequently blunt and relatively broader in the other species, particularly in A. maritima.

### Pollen

The pollen grains are normally tricolporate, and are fairly smooth which is characteristic of Artemisia, an anemophilous genus. According to investigations carried out by Straka (1952), Singh & Joshi (1969),

and Pragłowski (1971) the surface of the grains of A. maritima is furnished with very small, sparse spinuloid processes. The pollen grains are usually spheroidal to subprolate in all three species and contain three nuclei at maturity, the sperm nuclei being elongate, almost vermicular in shape.

In plants with meiotic irregularities, i.e. chiefly within A. maritima and to some extent A. santonicum, abnormal pollen grains are frequently found. The grains may be abnormal in size as well as shape. For example, giant pollen grains have been observed (Fig. 53 B, D). As was discussed earlier, these may be the result of restitution nucleus formation and would thus contain double the normal chromosome number. The fertility of these pollen grains has not been tested, but they appear to be morphologically well-developed, except that they often have a divergent number of colpi, and they stain in cotton blue.

More commonly twin pollen grains or pollen grains of subnormal size are observed in meiotically aberrant plants. In the latter case there are often only two colpi. Most of these pollen grains do not stain in cotton blue and are therefore probably infertile.

The breadth of 20 pollen grains (polar view) of each plant was measured, and the mean values obtained for the different plants were plotted in a graph (Fig. 52).

|                      |    | m    | s         |                                          |
|----------------------|----|------|-----------|------------------------------------------|
| <u>A. maritima</u>   |    | 22.1 | $\pm 1.8$ |                                          |
| <u>A. vallesiaca</u> |    | 19.0 | $\pm 1.1$ |                                          |
| <u>A. santonicum</u> | 2x | 16.7 | $\pm 1.3$ | Measurements in $\mu$<br>( $\pm 1 \mu$ ) |
|                      | 4x | 22.1 | $\pm 1.8$ |                                          |
|                      | 6x | 24.3 |           |                                          |

Ploidy level and pollen size are obviously correlated, although this is less distinct interspecifically than intraspecifically. Thus, the three ploidy levels of A. santonicum can be fairly easily distinguished on pollen size alone, at least diploids and polyploids. But the hexaploid A. maritima has usually pollen grains of about the same size as tetraploid A. santonicum, while A. vallesiaca, also tetraploid, has pollen grains of a smaller average size than both of them (Fig. 54). A similar condition in other Artemisia species is described by Ehrendorfer (1964). He observed that the closely allied species within the group Heterophyllae had on the average smaller pollen grains than the related group Norvegicae, the same ploidy levels compared.



## Pistil

Style. As was mentioned previously, the length of the mature style varies considerably in all three species. The stigmas are usually immediately above or below the level of the corolla mouth. Rarely the style is much shorter, but in many cases it protrudes as much as 0.5 mm beyond the corolla tube. Within the same plant variation in style length is slight, but the total variation in a population is often pronounced.

Stigma. The style is terminated by two stigmatic branches that become recurved only after the pollen is shed. The stigmatic branches are more or less flattened and papillate with especially long papillae towards the branch ends. There is some variation in stigma size both between and within species.

The length of the style branches was measured on five samples from each plant (Fig. 55).

|                         | m    | s          |                                       |
|-------------------------|------|------------|---------------------------------------|
| <u>A. maritima</u>      | 0.73 | $\pm 0.11$ |                                       |
| <u>A. vallesiaca</u>    | 0.80 | $\pm 0.09$ |                                       |
| <u>A. santonicum</u> 2x | 0.54 | $\pm 0.07$ | Measurements in mm<br>( $\pm 0.1$ mm) |
| 4x                      | 0.57 | $\pm 0.04$ |                                       |
| 6x                      | 0.66 |            |                                       |

A. santonicum, especially the diploids, clearly has shorter style branches than the other two species, and A. vallesiaca generally has the longest. There are some form series in A. maritima, however, with very long style branches (Fig. 56 D). Other form series in this species are characterized by their short style branches (Fig. 56 C).

Some abnormalities in style appearance have been observed very rarely in A. maritima and A. vallesiaca. Thus three-branched and even four-branched styles have been noted (Fig. 56 F, G, I), the abnormality usually being common to the majority of florets in a plant.

Ovary. The ovary is inferior and bicarpellate with a single locule and ovule. In A. vallesiaca the ovary is often markedly smaller and more rounded in outline than in the other two species. Such differences in size and shape can be more easily observed in the mature fruit, however.

## Fruit

No mature fruits of hexaploid *A. santonicum* have been available.

The achenes are more or less obovate in shape. The generally oblique style scar is sometimes (in *A. vallesiaca* rarely) surrounded by a bulge. The glabrous fruit surface is slightly sculptured with low longitudinal ridges of varying breadth.

The size of the achenes is of some diagnostic value as it is a direct expression of the different ploidy levels. Overlapping is extensive, however.

The length and breadth of ten achenes per plant was noted, and for each plant the mean values for length and the length/breadth ratio were plotted in graphs (Figs. 57, 58).

Length:

|                      |    | m    | s            |                                           |
|----------------------|----|------|--------------|-------------------------------------------|
| <u>A. maritima</u>   |    | 2.10 | <u>+0.24</u> |                                           |
| <u>A. vallesiaca</u> |    | 1.88 | <u>+0.18</u> |                                           |
| <u>A. santonicum</u> | 2x | 1.72 | <u>+0.14</u> | Measurements in mm<br>( <u>+0.05 mm</u> ) |
|                      | 4x | 1.89 | <u>+0.18</u> |                                           |

Though the mean values of the three ploidy levels are well separated there is great variation, especially in *A. maritima*. Note, for instance, the small-fruited ecotype of Öland/Gotland (Fig. 59 E, F). The values for tetraploid *A. santonicum* are of the same magnitude as for *A. vallesiaca*. However, if length is combined with other characters such as fruit shape and surface sculpture there will generally be no difficulty in separating the achenes of the three species.

Length/breadth ratio:

|                      |    | m    | s            |
|----------------------|----|------|--------------|
| <u>A. maritima</u>   |    | 2.24 | <u>+0.22</u> |
| <u>A. vallesiaca</u> |    | 1.79 | <u>+0.19</u> |
| <u>A. santonicum</u> | 2x | 2.23 | <u>+0.22</u> |
|                      | 4x | 2.24 | <u>+0.21</u> |

In *A. maritima* and *A. santonicum* fruits are usually of the same elongate shape and are rather easy to distinguish from the more rounded *vallesiaca* achenes.

The surface sculpture of the achenes of *A. vallesiaca* is also characteristic. The ridges are decidedly broader than in the other species. In *A. santonicum* the ridges are generally very narrow, but this also applies to some *maritima* form series (Fig. 61).



|                      |    | m   | s          |                       |
|----------------------|----|-----|------------|-----------------------|
| <u>A. maritima</u>   |    | 80  | <u>+14</u> |                       |
| <u>A. vallesiaca</u> |    | 114 | <u>+16</u> |                       |
| <u>A. santonicum</u> | 2x | 60  | <u>+9</u>  | Measurements in $\mu$ |
|                      | 4x | 62  | <u>+14</u> | ( <u>+10</u> $\mu$ )  |

## CONCLUSIONS

There is a wide range of variation in most morphological characters. Some phenetic variation seen in nature is modificational, but after growing plants under uniform conditions it was apparent that a great deal of the variation is hereditary. Overlapping between species is often pronounced, and though many of the quantitative characters more or less reflect the different ploidy levels, e.g. size of stomata, phyllaries, corolla tubes, stamens, pollen grains and achenes, the correlation between size and ploidy level is less distinct interspecifically than intraspecifically. Still, if as many characters as possible are taken into consideration there will generally be no difficulty in identifying the species. Cytological observations will further support identification.

The populations in the saline areas of central Germany and on the Baltic coast of Germany have been of special interest in this investigation, as they have been distinguished as a separate taxon of the Artemisia maritima complex by many authors. Willdenow (1803 p. 1834) gave it species rank, calling it Artemisia salina. It is evident from his indication of the area of distribution in the description and from herbarium sheets determined by him that he also incorporated material from Hungary in this species, i.e., part of what is now considered as A. santonicum L. Another part, comprising Hungarian forms with erect branches and capitula, was considered by Willdenow to be conspecific with A. monogyna Waldst. & Kit. The type in the Willdenow herbarium (B, lectotype, see Taxonomy) originates from central Germany, however.

Also more recent authors, such as Sagorski (1907, 1908), have confused the central German and Hungarian taxa and treated them as one taxon or as subunits within one taxon. The present investigation

has made it evident that "A. salina" from central and Baltic Germany is conspecific with A. maritima L. This conclusion is based on cytological and morphological observations. Kawatani & Ohno (1960) arrived at the same conclusion after a cytological and phytochemical study of cultivated material originating from two seed collections from Artern in central Germany.

The confusion that has prevailed between A. santonicum and "A. saline" is probably due to a certain similarity in general habit. The central German populations in particular are sparsely pubescent with the basal parts soon becoming glabrescent, and the leaves wither soon after or even before the onset of anthesis. These characters are also distinguishing for A. santonicum. However, in all other characters (shape of leaves, capitula, florets etc.) it is apparent that the populations from central and Baltic Germany show great affinities to the populations on the coast of south-western Sweden (Skåne) as well as to the North Sea populations of A. maritima, which will be shown in the next section. The chromosome number of "A. salina" is 54 as in A. maritima and the Greek A. santonicum, but the general appearance of the karyotype is more like that of the former species.



## VARIATION WITHIN TAXA

In all three species, especially in A. maritima, patterns of local variation seemed to be superimposed on the general state of polymorphism. In many cases populations apparently contained the same polymorphic types though differing in frequency of occurrence of the morphological features. Some of the characters or character combinations are probably of adaptive importance, i.e. the local races are adapted to their respective environments, which are very varying in different parts of the area of distribution, especially for A. maritima. Because of these and other problems, e.g. the origin of polyploid A. santonicum, the author considered it appropriate to make more detailed studies of the variation at population level, for instance, and if possible to establish discontinuities in the whole variation range in order to distinguish subunits within the taxa. The results of these detailed investigations will be presented in this section.

## ARTEMISIA MARITIMA

### Variation at Population Level of Some Characters Often Used for Subdividing the Species

Characters such as "drooping branches and capitula", "highly suffruticose stems", "stems glabrous basally" are often met with in floras as sole descriptions of subunits within A. maritima. Thus A. maritima var. suffruticosa Hartweg (1820 p. 309) is described as richly branched with more or less erect branches and drooping heads, and less grey and aromatic than the "typical" maritima. As a rule geographical distribution is not mentioned, but the diverging subunits distinguished are described as growing more or less intermingled with the "type". The authors of floras frequently misinterpret species named by earlier authors, e.g. A. salina Willd. and A. gallica Willd., and use the names for ma-

ritima forms within any geographical area. Thus Liljeblad (1816 p. 459) applied "A. salina" to Swedish material, but his taxon is largely conspecific with the variety mentioned above described by Hartman. Koch's (1837 p. 369) only description of "var. salina" is "flores penduli", etc.

In the previous section the author demonstrated the extensive variation within the species of the characters mentioned. It seemed worthwhile studying the variation within a single population and comparing it with that of the species as a whole. Therefore, three geographically separated populations were chosen, and twenty plants per population were grown in cultivation and investigated in the following characters:

- a) Degree of suffrutescence
- b) Degree of stem pubescence
- c) Synflorescence symmetry
- d) Degree of branch rigidity
- e) Position of capitula on branches
- f) Number of capitula per unit of branch length
- g) Peduncle length

a--e: classification as in the previous section (pp. 29, 35, 36, 37).

f--g: observations were made on branches in the middle of the synflorescence.

The populations investigated were from the following localities:

- I) Sweden, Skåne, Skanör
- II) Denmark, Sjaelland, Roskilde
- III) Denmark, Jylland, Esbjerg

Results. Each character shows a wide range of variation in all three populations (Fig. 62), as in most populations seen by the author. Variation is more or less continuous within a population as there are no distinct boundaries between the groups in a--e. For instance, within the same population there may be plants with erect or pendulous branches and several transitional forms, or plants with various degree of suffrutescence or pubescence, etc., although there is usually a certain optimum. Likewise, there is no uniformity of number and position of the capitula either within populations or within the species as a whole. None of the different forms are in any way geographically isolated from one another, there thus being every chance of genetic interchange. Obviously to subdivide the species solely on such characters is extremely hazardous. The characters



will be useful only in combination with one another and with more "stable" characters (i.e. these varying less within populations), e.g. many floral characters, as will be shown in the next section.

Scent. The difference in scent between the so-called subspecies or varieties is often pointed out. Thus "A. salina" sensu Liljeblād and A. maritima var. suffruticosa Hartman (and others) are described as being less aromatic than the typical maritima forms. As these varieties are described as differing only in suffrutescence, pubescence and branching system it should be possible to find some correlation between these characters and plant odour, which arises from the presence of certain aromatic substances, santonin or related substances. These are found in most species of subgenus Seriphidium (see e.g. Ferri 1964) and are considered to be mainly produced in the glandular hairs which are so abundant especially on the flowers.

The author investigated cultivated material of A. maritima to see if there was the correlation mentioned. No correlation was found relying on odour alone, nor could any correlation be observed between the morphological characters concerned and gland frequency. It may thus be concluded that scent is of little value as a diagnostic character within A. maritima.

### Analysis and Comparison of Variation in Nine Grand Populations

Introduction. To provide a possible means of subdivision of the species nine grand populations (grand population: a group of local populations with a similar habitat from a limited area) were subjected to a detailed morphological analysis. Between several of the grand populations no gene exchange was possible because of geographical isolation. The Danish islands, the Baltic coast of Germany, Great Britain and the coasts of the Channel on the Continental side southwards to south-western France were excluded from the investigation, on the following grounds (partly based on preliminary observations):

- 1) The material from the coasts of eastern Denmark, Baltic Germany and Skåne (Sweden) showed clear affinities and could be treated as a

unit. The populations from Skåne were chosen as being representative.

2) The Continental North Sea material could be treated as a unit as the area of distribution is continuous from Jylland to the IJsselmeer. Even so the area is large, and some groups of populations were selected and compared primarily to establish the presumed affinities.

3) At the time of the investigation no living material was available from Great Britain, the south-western Netherlands or France. Later, material from France and Great Britain was collected and analysed morphologically, and the results were compared with the rest of the investigation. They were not included in the main statistical analysis, as it was necessary to use material from the same growth season to ensure that external conditions were as nearly uniform as possible. The French and British collections comprised four grand populations, representing the Continental Channel coast, south-western France and eastern and south-western England.

The nine grand populations used. 40--50 plants (in the case of B, H and J 20--30) from each of the following areas were chosen at random, grown under uniform conditions, and then investigated morphologically for one growth season (map Fig. 63).

- A. Western Skåne, Sweden (representing 13 populations). Marsh, soft clay or silty mud.
- B. Halland, Sweden (5 populations). Marsh, muddy sand.
- C. Southern Bohuslän archipelago, Sweden (7 populations). Rocky islands and skerries.
- D. Öland and Gotland, Sweden (13 populations). Low flat shores, thin layer of soil on limestone.
- E. South-western Jylland, Denmark (7 populations). Marsh, muddy sand.
- F. Nordfriesland, Germany (8 populations). Mostly extensive marshes, sandy clays.
- G. Ostfriesland, Germany (7 populations). Mostly extensive marshes, firm clayey soils.
- H. Friesland, the Netherlands (5 populations). Polder (reclaimed land), heavy clays.
- J. Artern, Thüringen, central Germany (1 population). Saline spring, soils rich in humus.



In B, H and J the material is more limited, and it is to be expected that the dispersion values (standard deviation) in these cases will be higher than if the material had been as extensive as in the other cases. However, this effect is more than neutralized by the effect of the smaller number of populations (= a presumably narrower range of variation) represented in B, H and J, as will be shown later.

As a comparison to the populations from A--J, 20--30 plants from each of the following areas were grown under uniform conditions and analysed.

N Fr. Somme--Calvados, France (representing 3 populations). Extensive marshes in estuaries, sandy muds and clays.

S Fr. Vendée--Charente-Maritime, France (4 populations). Small marshes along ditches in salines, muddy clays.

E Engl. Norfolk--Essex, England (5 populations). Large marshes, soft muddy clays.

W Engl. Somerset, England (2 populations). Small narrow marshes, muddy sand.

Morphological characters used. The following 32 characters have been studied.

|                            |                                              |
|----------------------------|----------------------------------------------|
| Leaves                     | lamina length                                |
|                            | length/breadth ratio of lamina               |
|                            | degree of segmentation                       |
|                            | breadth of leaf segment                      |
|                            | breadth/length ratio of leaf segment         |
| Stem and<br>synflorescence | stomatal length                              |
|                            | shoot length                                 |
|                            | suffrutescence                               |
|                            | pubescence                                   |
|                            | synflorescence length/shoot length ratio     |
|                            | branch rigidity                              |
|                            | synflorescence symmetry                      |
|                            | degree of branching                          |
|                            | number of capitula per unit of branch length |
|                            | position of capitula on branches             |
| Capitula                   | peduncle length                              |
|                            | phyllary pubescence                          |
|                            | breadth of inner phyllaries                  |
|                            | breadth/length ratio of inner phyllaries     |
|                            | number of florets per capitulum              |

|         |                                          |
|---------|------------------------------------------|
| Corolla | corolla length                           |
|         | corolla length/corolla lobe length ratio |
|         | length/breadth ratio of corolla lobe     |
|         | number of glands on corolla              |
| Stamens | theca length                             |
|         | length of connective appendage           |
|         | pollen size                              |
| Pistil  | style length                             |
|         | length of style branch                   |
| Fruit   | achene length                            |
|         | length/breadth ratio of achene           |
|         | breadth of achene ridges                 |

The nine grand populations showed affinity in many characters. As the aim of the investigation was to record possible differences and discontinuities, the results for characters in which the nine groups showed affinity in all combinations are not shown here.

Statistical methods used. Only continuous variates were statistically analysed. The mean value ( $m$ ) and standard deviation ( $s$ ) were calculated.

For the statistical analysis a normal distribution of the quantitatively varying characters in question is a necessary prerequisite. Deviations from the normal distribution are sometimes apparent, but as these deviations are small, the statistical method can still be considered acceptable for the evaluation and comparison of variation within the grand populations.

The grand populations were compared pairwise (A with B, A with C, B with C etc.). The standard error ( $sE$ ) for each of the two mean values was calculated on the basis of an average value for  $s^2$ :

$$s_{av}^2 = \frac{S(x - m)_A^2 + S(x - m)_B^2}{(n - 1)_A + (n - 1)_B}$$

$$sE_A^2 = \frac{s_{av}^2}{n_A}$$

$$sE_B^2 = \frac{s_{av}^2}{n_B}$$

The standard error for the difference between the mean values is



$$sE_{diff} = \pm \sqrt{sE_A^2 + sE_B^2}$$

$$t = \frac{m_A - m_B}{sE_{diff}}$$

The level of significance of the difference between the mean values is used as an index of the affinity between the two populations for the character in question.

|                 |                             |
|-----------------|-----------------------------|
| P > 5 %         | no significance             |
| 5 % > P > 1 %   | <sup>x</sup> significance   |
| 1 % > P > 0.1 % | <sup>xx</sup> significance  |
| 0.1 % > P       | <sup>xxx</sup> significance |

That is, for each morphological character treated, the greatest dissimilarities exist between two populations with mean values different with a <sup>xxx</sup>significance. This may apply if: 1) the mean values are rather close but dispersion small, and 2) dispersion is greater but mean values are very well separated. It must be pointed out that the indices obtained for different morphological characters cannot be directly compared, as the exact diagnostic usefulness of each character is difficult to assess and at least cannot be given a precise value that can be used in comparisons with other characters. The indices will only indicate where the greatest or smallest differences are situated in the material as regards the morphologic character in question.

In the maps degree of affinity is illustrated by means of lines connecting the two localities in the pair compared. A broad line means that the mean values are not significantly different, a thin line that they are <sup>x</sup>significantly different, and a dashed line that they are <sup>xx</sup>significantly different. Where there is no connecting line at all the mean values are <sup>xxx</sup>significantly different.

Leaves. The length/breadth ratio of the leaves is similar throughout the material, usually varying between 1.6 and 2.6. A tendency towards more elongate leaves can be discerned in plants from Bohuslän, Halland and north-western France, while leaves somewhat more rounded

in outline may be found in populations from Skåne, Öland--Gotland, the northern Continental North Sea coast and Artern. There is also some variation in leaf shape depending on where the broadest part of the leaf is. Thus, in plants from Öland--Gotland the leaves are broadest in the middle, in plants from Bohuslän the leaves are broadest in the basal part of the lamina.

More distinct local patterns of variation are apparent in length of leaf laminae as well as in degree of segmentation and in size and shape of leaf segments.

Lamina length (Fig. 64). The material from Öland--Gotland is conspicuous in having extremely small leaves. Leaf length is fairly uniform in the rest of the material. There is a tendency towards longer leaves than the average in Skåne and Bohuslän, but the respective values of standard deviation are high, i.e. there is a substantial representation of small as well as large leaves in both cases.

In the populations from England and northern France the leaves are evidently somewhat smaller than average on the North Sea coast, while in the plants from south-western France they are usually longer. The mean values are fairly close, however (between 20 and 30 mm, as in the rest of the material except that from Öland--Gotland).

Segmentation (number of segments/length of longest primary segment, Fig. 65). The leaves are usually 2--3-pinnatisect, seldom 4-pinnatisect. There is considerable variation in the number of ultimate segments as related to leaf size, especially in the northern North Sea populations (E--H). A noticeable high degree of segmentation is found in material from Ostfriesland, north-western France and, especially, the inland locality in central Germany (J). The Swedish material on the whole has less divided leaves than the Continental and English. As is evident from the diagrams (- 2s give negative values, see Fig. 65), the values of leaf segmentation do not have a strictly normal distribution. Moreover, the range of variation is wide in most cases, so that degree of segmentation is not very useful as a diagnostic character.

#### Shape and size of leaf segments.

Breadth/length ratio (Fig. 66): The ultimate leaf segments are more or less linear in shape. The segment apices are generally subacute, but as a rule the segments do not taper evenly towards the point. Instead they tend to be spatulate in outline, i.e. the segment is broadest near the apex. This is particularly pronounced



in the material from western Sweden (B, C; Fig. 25 B, C) and in some of the plants from Öland--Gotland (D; Fig. 25 D). The latter are also distinguished by the usually blunt apices of the leaf segments which are furthermore very short in relation to their breadth, a condition that is apparent in many French and English populations, too. Other populations distinguished by the breadth/length ratio of the leaf segments are A (Skåne) and E (S.W. Jylland), which have unusually narrow segments tapering evenly to an acute or subacute apex (Fig. 25 A, F). Extremely long and narrow leaf segments have been observed in some populations of plants with long internodes, sparse synflorescences and small narrow capitula (e.g. coll. no. 61, Figs. 18 K, 25 E).

**Breadth (Fig. 67):** The absolute breadth of the secondary segments is more or less the same (c. 0.6 mm) in all non-British populations except in Bohuslän (C) and parts of France, plants from these two areas having very broad leaf segments, usually more than 0.7 mm and not seldom around 1 mm. Thus, both the breadth and the shape of the segments distinguish the populations from Bohuslän and France from the remainder of the maritima material.

The English plants also have leaf segments that are somewhat broader than the average, though the mean values do not exceed 0.7 mm and the dispersion is large, at least in the material from western England.

**Stomata (Fig. 68).** All measurements were made on leaves on lower third of the stem.

Spontaneous material is especially unsuitable for studies on variation of stomatal length, as the length of the guard cells is particularly modificative. Discontinuities in length variation, if any, are difficult to discern. However, in cultivation under uniform conditions real differences in stomatal length will show up (Fig. 69).

There is a slight tendency for populations from more saline habitats to have smaller guard cells than populations from brackish habitats. Thus, in D (Öland--Gotland) stomatal cells are rather long, while in C (Bohuslän), G (Ostfriesland) and H (the Netherlands) they are comparatively small. Conspicuously small guard cells distinguish the Artern population (J), which grows on a substrate in which the concentration of soil salts often rises considerably due to an arid climate. The stomatal cells of J are of less than average size even in the spontaneous material.

Stem and inflorescence. Shoot length (Fig. 70). The greatest variation in shoot length is found within the Swedish, French and English populations (note high dispersion values). Still, two groups of these populations are significantly different from the rest of the material: C (Bohuslän) with shoots taller than the average, and D (Öland--Gotland) with shoots much shorter than the average. Many of the D plants are only about 10 cm high. Rather short plants may also be found in B (Halland), but this is not the rule.

The average shoot length in the non-Scandinavian populations fluctuates around 30--35 cm, the higher values being found in the French and inland material where dispersion is also considerably wider, however.

Shoot morphology (Fig. 72). The nine grand populations as well as the French and the English material were investigated with respect to some of the shoot-morphologic characters often used in taxonomic delimitation. The same classification into groups previously mentioned in this paper (pp. 29, 35, 36, 37) was employed. The frequencies of occurrence (in %) are shown in histograms.

Variation is great in all characters and in all populations. A few more or less distinct differences between the populations can be observed, however.

Suffrutescence: Stems of C plants (Bohuslän) are generally more lignified, D plants (Öland--Gotland) less lignified than the average. Most plants in other populations are moderately suffrutescent.

Pubescence: Some of the French populations, as well as B (Halland), C (Bohuslän) and especially D (Öland--Gotland) are generally more densely pubescent (whitish) than the other populations, which are mostly moderately pubescent (grey). Rather sparsely pubescent (greyish-green) plants are to be found chiefly in Artern (J), Skåne (A) and England. In J the plants are often glabrous at the base but pubescent in the upper parts.

Branch rigidity: No great differences in variation in degree of branch rigidity were observed, except that totally erect branches are most usual on Öland and Gotland, in Artern and in France. The northern North Sea populations (E--H) contain the highest proportion of plants with wholly pendent branches.

Synflorescence symmetry: Degree of symmetry of the branching system varies greatly in all populations. The synflorescence is generally somewhat secund, though in Artern the majority of the



plants have branches diverging in all directions.

Branching system: The following classification into groups was made.

- 1 No branching, peduncles of primary order
- (2) Primary branches, single terminal capitula
- 2 Primary branches, peduncles of secondary order
- 3 Secondary branches, peduncles of tertiary order

The branching system is usually of a primary or secondary order (with peduncles of a secondary or tertiary order). Simple synflorescences are characteristic of plants on Öland and Gotland and in Halland. In these two populations no secondary branching at all has been found, in contrast to the other populations.

Capitula. There is some variation in the size of the heads owing to factors such as length and breadth of phyllaries and number and size of florets. Very large heads with long and broad phyllaries are found in the populations from Bohuslän and in some French and English populations (Fig. 33 C, I, K), while plants from Öland--Gotland are characterized by small compact heads with short and rather narrow phyllaries (Fig. 33 D, E). Most of the populations have more or less blunt phyllaries with rather broad scarious margins. The herbaceous parts of the phyllaries are always somewhat glandular-pubescent. The density of the pubescence varies considerably, largely complying to the same pattern as that of the stem pubescence. Thus, more or less densely pubescent phyllaries are found particularly in Halland (B), Bohuslän (C) and on Öland and Gotland (D), whereas in Skåne (A) and Artern (J) there are often only scattered tufts of hairs on the upper parts of the phyllaries.

Breadth of inner phyllaries (Fig. 73). Statistical analysis of one of the varying characters of the phyllaries, viz., breadth of the inner phyllaries, proved what has already been said about phyllary size, especially in the case of Bohuslän and France. The mean values for these populations were significantly higher than all others. The lowest values are to be found in the populations from Artern and in some of the northern North Sea populations, and further in the D populations (Öland--Gotland), in which the phyllaries are also the shortest.

Number of florets per capitulum (Fig. 71). The number of florets per head usually varies between 3 and 11. There is no distinct pattern of variation other than the fact that except for Öland--

Gotland (D) there are generally more florets per head in the Scandinavian material (c. 5--11) than in the non-Scandinavian (3--7). Especially plants from Bohuslän (C) have many-flowered heads. In the coarctata forms, which occur in all grand populations, the number of florets may be very high owing to the fusion of several heads into larger aggregates.

Floret. The absolute length of the corolla varies within certain limits in all populations, but there is no definite trend in any direction except that the populations from Öland--Gotland have somewhat smaller florets than the average, and on the whole it seems that in Scandinavian populations florets exceeding 3.0 mm occur less frequently than elsewhere. The size and shape of the corolla lobes also vary somewhat, especially the latter. The most distinct variation patterns were provided by the corolla length/corolla lobe length ratio and length/breadth ratio of the corolla lobe.

Corolla length/corolla lobe length ratio (Fig. 74). The Swedish populations have corollas with deeper incisions than the northern North Sea, French and English populations. Thus, two distinct groups can be distinguished in the material. The plants from the inland locality (J) show resemblance to the Swedish populations.

Length/breadth ratio of corolla lobe (Fig. 75). In this respect, too, the northern North Sea populations form an affinity group, to which the material from Skåne is allied. The western English material may also be classified in this group. The corolla lobes of these populations are generally narrowly triangular, almost lanceolate, whereas D (Öland--Gotland) and especially B (Halland) and C (Bohuslän) have broadly triangular lobes. The plants from Artern, France and eastern England are intermediate.

Glands. The corolla tubes are more or less glandular in the whole material. Variation in gland frequency is random, i.e. no population group has been observed to be significantly different from any other. The glands are of the same general type (Fig. 47 A--F) in all populations.

Stamens. The thecae vary in length within certain limits common to the whole material, but short thecae are most frequent in the populations from Öland and Gotland. There is a slight variation between populations in size of connective appendages. In most of the material stamens bear appendages 0.32--0.36 mm long. In plants from Halland appendages are usually somewhat longer (and also broader),



in those from Öland--Gotland somewhat shorter (Fig. 76). Dispersion values are rather high in all cases, however, a fact that reduces the taxonomic value of this character.

Pistil. Style length. The style varies considerably in length throughout the material. The stigmas are as often beneath as above the level of the corolla mouth in all populations.

Length of style branch (Fig. 77). The style branches are usually between 0.70 and 0.80 mm long. Only plants from Öland and Gotland have shorter branches (Fig. 56 C), significantly shorter than many of the other populations. Conspicuously long style branches (0.90--1.0 mm) have been observed in material from Bohuslän, Jylland and England (Fig. 56 B, D).

Ovary size. There is some variation in ovary size, but as the ovary changes rapidly in size as it matures, to compare measurements within the material would be inadvisable. Therefore only mature fruits have been measured for further statistical analysis.

Fruit. The achenes are in all cases obovate, less narrowly pyriform in the populations from western Sweden, Öland--Gotland and Artern than in the rest of the material. The outline in fruits from Bohuslän is often even convex in the basal part rather than slightly concave as in the "typical" maritima achene.

Achene length (Fig. 79). Plants from Öland and Gotland (D) generally have distinctly smaller fruits than the rest of the material. The D achenes are only c. 1.8--1.9 mm long, as compared with the other populations where the achenes are generally 2.1--2.2 mm long.

The achene surface is sculptured, with low longitudinal ridges, and sometimes a bulge surrounds the style scar.

Breadth of achene ridges (Fig. 78). The breadth of the ridges is not correlated to fruit size. Thus, the populations from Halland and Bohuslän, which generally have large fruits, nevertheless have the narrowest ridges. English fruits have also rather narrow ridges. The differences in breadth between the other populations are practically negligible.

Conclusions. Mention was made earlier (p. 17) of the fact that even in large populations and although Artemisia maritima is wind-pollinated the panmictic units are probably not very large. This will mean that some racial differentiation can be expected to develop

at least within regions if not locally. This regional differentiation will be retarded in large continuous populations on account of occasional long-range dispersal. Such large continuous populations within A. maritima are found in the North Sea area in particular, but also in parts of England, Skåne and the Danish islands.

But populations in different parts of the area of distribution are generally also exposed to differences in environment (e.g. substrate, salinity, tidal variations, climate), and are thereby subject to differential selection. If the populations are geographically isolated, natural selection will act in combination with this spatial, and thus reproductive, isolation. Such isolated subgroups are also characteristic of certain parts of the area of distribution, above all Öland--Gotland and central Germany. The western Swedish populations (Bohuslän--Halland) and some French and English population groups are also more or less isolated from the rest of the area of distribution.

Many of the characters or character combinations investigated are probably of adaptive significance, e.g. certain vegetative characters. Thus, the small compact growth form together with the dense pubescence characteristic of the plants on Öland and Gotland is probably an adaptation to the special environmental conditions that prevail on these islands. The climate is rather arid, and the irregularity of precipitation pronounced (cf. Pettersson 1965 p. 131). Furthermore, as the soil layer is generally thin, water economy is often critical. The wide flat type of landscape is much exposed both to winds and precipitation. The small-statured habit of A. maritima in these areas are typical for many other species and species forms on the islands.

Another feature of the regional morphological variation is that the characters often vary independently, as, for instance, achene size and breadth of achene ridges, corolla length and length of corolla lobe, and length of leaf lamina and breadth of leaf segment. It is very difficult to discern a definite pattern in the overall infra-specific variation as this is often of the type box-in-box differentiation. Many populations are probably polymorphic for the same alleles but the alleles are present in different frequencies.

If for each population the number of characters in which the mean value of the population was found to be significantly (xx and xxx) different is counted, the final sum will give an idea as to where the greatest discontinuities in the material are situated. It is



also possible to compare a certain group of grand populations with another group etc. (Fig. 80).

The morphological characters were divided into two groups: 1) vegetative characters and 2) floral characters.

Each grand population compared with the rest of the material (Table 6). It is evident that C (Bohuslän) and particularly D (Öland--Gotland) occupies an exceptional position. The sum total of significant differences is largest in D for both vegetative and floral characters. Furthermore, D plants have a characteristic habit, such as degree of pubescence, suffrutescence, branching and branch rigidity (not statistically analysed; Fig. 72). C, too, has certain distinguishing shoot morphologic features, e.g. degree of pubescence and suffrutescence, but the population is not so characteristic in general habit as D.

Other smaller discontinuities can be discerned in A (Skåne) and J (Artern), and to some extent also in B (Halland), at least as regards vegetative characters.

Comparisons between populations. 1) The northern North Sea populations (E--H) are much alike as would be expected as the distribution is continuous from Jylland to the Netherlands. Note that the material from the Netherlands (H) represents a smaller number of populations than each of E--G and thus probably a smaller range of variation. The effect of this is that in this investigation H differs significantly from the other populations in more characters than does G (Ostfriesland), despite the fact that G and H are so alike that there are no significant (xx and xxx) differences between them.

2) The southern Scandinavian populations (A) resemble the northern North Sea material vegetatively, but there are a number of differences in floral characters.

3) The two grand populations from western Sweden (B and C) are very much alike in floral characters, and though some differences in vegetative characters do exist, I have chosen to unite the two groups in one "form series". This form series is distinguished at least in floral characters from the populations A and E--H, from which it is also isolated geographically. As regards vegetative characters the B and C populations are not so well defined, and in nature differences in those characters are furthermore often obscured by modifications rendering identification more difficult. The use of subspecific rank is perhaps justified though in the author's opinion impracticable.

4) The populations from Öland and Gotland (D) constitute an especially well-defined group within A. maritima, characteristic both in habit and floral characters. The group is geographically isolated from the rest of the material. As to whether it would also prove to be reproductively isolated if confronted with the other material can be determined from crossing results, though even morphological investigation supports subspecific rank for the group.

5) The inland population (J) of Artern, central Germany is geographically isolated and has also developed certain characters that distinguish it from the rest of the material. These characters are few, however, and mostly vegetative. Furthermore, as the material represents only one population and thus a probably more restricted range of variation than in each of the populations A--H (the value of *s* is lowest in J for many characters), the number of significantly different characters may be somewhat exaggerated in relation to the remainder of the grand populations. The proportionately narrow range of variation may, of course, also reflect a true condition, but this seems less probable judging from herbarium material from the area. This seems to be as variable as material from other areas, and besides, a large number of varieties and forms have been described by Śagorŝki (1908) and others.

In general the J population is rather like the southern Scandinavian populations and, in particular, the northern North Sea populations.

6) As regards the populations that were not included in the statistical investigation, viz., those from France and England, the following observations can be made:

In floral characters the French and English populations are mostly like the northern North Sea populations (E--H), but variation is great. Thus the florets and achenes resemble those found in E--H except that the corolla lobes are generally not so elongate, the connective appendages are as often rather short as they are long, and the achene ridges are frequently rather narrow, at least in the English material. The French populations in particular occasionally have very large heads, like those in Bohuslän, owing more to very broad and long phyllaries than to the number of florets per head which is moderate as in E--H.

Variation in vegetative characters is great compared with the rest of the material. Thus, leaf segment breadth varies from moderately narrow as those found in E--H, to very broad. Segments as



broad as but not as long as those observed in Bohuslän may be found particularly in France, more seldom in England. In characters of shoot morphology the two population groups are fairly like E--H though very densely pubescent plants are more usual in France, while greyish-green plants like those found in Skåne and Artern are more usual in England.

The differences between the two French subgroups, which are geographically isolated from each other by the Breton peninsula, are not great. Plants from north-western France are generally somewhat more densely pubescent, the leaves are more segmented, shorter and have broader segments, and the capitula are larger with broader phyllaries than in plants from south-western France.

A comparison of the two English subgroups shows that the plants from eastern England seem to have more richly branched synflorescences, longer leaves, larger heads with broader phyllaries, and more broadly triangular corolla lobes than those from western England, but the differences are slight.

## ARTEMISIA VALLESIACA

Swiss and Italian Populations Compared

Material: 172 plants (12 populations) from Switzerland

31 plants (2 populations) from Italy

The plants were cultivated under uniform conditions and then investigated morphologically. Mean value (m) and standard deviation (s) were calculated for each quantitatively varying character.

Leaves. The cauline leaves are nearly always sessile in the Italian plants and highly pinnatisect even within the synflorescence, whereas Swiss plants often have distinct petioles and auricles, and the upper leaves are simpler in structure, often entire (Fig. 19 A--D). Furthermore, the ultimate leaf segments are more elongate in Italian populations than in Swiss.

Breadth/length ratio of secondary leaf segments (Fig. 81 A):

|                | m    | s          |
|----------------|------|------------|
| Swiss plants   | 0.12 | $\pm 0.03$ |
| Italian plants | 0.07 | $\pm 0.02$ |

The Swiss plants have slightly smaller leaf stomata than the Italian ones, though overlapping is extensive (Fig. 81 B):

|                | m    | s         |                                                   |
|----------------|------|-----------|---------------------------------------------------|
| Swiss plants   | 27.9 | $\pm 2.2$ | Length of guard cells in $\mu$<br>( $\pm 1 \mu$ ) |
| Italian plants | 30.1 | $\pm 2.2$ |                                                   |

Capitula. The prominently mucronate outer phyllaries with basally broad scarious margins are typical of the Italian plants (Fig. 34 C), but also in some Swiss plants the phyllaries tend to be of this type. In general the phyllaries and scarious margins are broader in Italy.

Breadth of inner phyllaries (Fig. 81 C):

|                | m    | s          |                                       |
|----------------|------|------------|---------------------------------------|
| Swiss plants   | 1.16 | $\pm 0.19$ | Measurements in mm ( $\pm 0.1$<br>mm) |
| Italian plants | 1.42 | $\pm 0.17$ |                                       |

Breadth of scarious margins (Fig. 81 D):



|                | Outer phyll. |            | Inner phyll. |            |                                       |
|----------------|--------------|------------|--------------|------------|---------------------------------------|
|                | m            | s          | m            | s          |                                       |
| Swiss plants   | 0.24         | $\pm 0.12$ | 0.35         | $\pm 0.10$ | Measurements<br>in mm ( $\pm 0.1$ mm) |
| Italian plants | 0.46         | $\pm 0.13$ | 0.44         | $\pm 0.10$ |                                       |

The heads are generally larger in the Italian plants, not only because of the broader phyllaries but also because the number of florets per capitulum is greater (Fig. 81 E):

|                | m   | s         |
|----------------|-----|-----------|
| Swiss plants   | 4.7 | $\pm 1.3$ |
| Italian plants | 7.0 | $\pm 1.0$ |

Floret. Corolla tubes in Swiss plants tend to be longer as compared with Italian plants, but all length/breadth ratios are similar. Nor is there any difference in colour variation or gland frequency.

Corolla length (Fig. 81 F):

|                | m    | s          |                                       |
|----------------|------|------------|---------------------------------------|
| Swiss plants   | 2.86 | $\pm 0.19$ | Measurements in mm<br>( $\pm 0.1$ mm) |
| Italian plants | 2.50 | $\pm 0.12$ |                                       |

Stamens. The stamens are of the same general appearance and size in both population groups. The only dissimilarity observed is that the connective appendages are generally more than 0.30 mm long in Swiss plants, less than 0.30 mm long in Italian. Overlapping is great, however (Fig. 82):

|                | m    | s          |                                        |
|----------------|------|------------|----------------------------------------|
| Swiss plants   | 0.32 | $\pm 0.03$ | Measurements in mm<br>( $\pm 0.05$ mm) |
| Italian plants | 0.29 | $\pm 0.04$ |                                        |

Conclusions. The Swiss and Italian populations of A. vallesiaca are isolated from each other by the Pennine Alps. Only high passes connect the areas of distribution, and there is probably no gene exchange between the two population groups. During parts of the Late-glacial and early Post-glacial periods the areas of distribution were undoubtedly much larger and were also possibly connected, but during the long period of isolation since then certain morphological characters have developed somewhat differently in appearance or size in the two groups. The differences are mostly insignificant, and in general habit the populations are much alike and can thus not be accorded subspecific rank.

## ARTEMISIA SANTONICUM

Diploids, Tetraploids and Hexaploids Compared

Material: Diploids 51 plants (7 populations) from Austria  
                   5 plants (1 population) from Czechoslovakia  
           Tetraploids 19 plants (2 populations) from Roumania  
                   5 plants (1 population) from Hungary  
           Hexaploids 8 plants (1 population) from Greece

The plants were cultivated under uniform conditions and then investigated morphologically. The mean value was calculated for each quantitatively varying character.

Leaves. The three cytotypes all differ in size and shape of leaf laminae. The length of the laminae usually increases with degree of polyploidy (Fig. 83 B) as does the breadth, though to a lesser extent (Fig. 83 C). The diploids thus have very small leaves, especially the plants from Czechoslovakia, while the polyploids generally have much longer and more elongate leaves. In the polyploids variation is great, however, particularly in the tetraploids so that small-leaved forms are not infrequently found in Hungary, for instance.

In other leaf characters there is distinct dissimilarity between diploids and polyploids. In diploids the leaves have a higher degree of segmentation (Fig. 83 D), and the ultimate segments are much narrower, around 0.5 mm, while in polyploids the segments are c. 0.7 mm broad (Fig. 83 E) and somewhat shorter in relation to their breadth than in diploids.

The size of the guard cells of the leaf stomata reflects the ploidy level as diploids have much smaller stomata than polyploids (Fig. 83 F), but there are great similarities between the two polyploid cytotypes.

Stem and synflorescence. As regards shoot length diploids and hexaploids display the greatest resemblance, tetraploids usually having a wider range of variation (Fig. 83 A). The part of the shoot that is branched, i.e. that comprises the synflorescence, comprises c. 60 % of the total shoot length in diploids and tetraploids, only c. 50 % in hexaploids.



In other characters of shoot morphology the greatest similarities are to be found between the two polyploid cytotypes. Exceptions are pubescence and synflorescence symmetry: the hexaploids are slightly more densely pubescent and have more often asymmetric synflorescences than the others. Similarities between tetraploids and hexaploids exist in degree of branch rigidity (often more or less pendent branches), density and position of capitula, peduncle length (mostly shorter than in diploids!), breadth of inner phyllaries, and number of florets per head (Fig. 84).

Floret. The mean values for corolla length in the three cytotypes are all different, being smaller in hexaploids than in tetraploids (cf. shoot length!). However, the frequency polygons depicting the variation in the polyploids more or less cover one another (Fig. 85 A). The part of the corolla that is lobed is shorter in the tetraploids than in the others, the values for the diploids and hexaploids being uniform (Fig. 85 B). But as regards shape of corolla lobe tetraploids and hexaploids are more alike with slightly more broadly triangular lobes than the diploids.

The number of glands on the florets is greatest in the hexaploids, not only in absolute figures but also per square mm (cf. Figs. 85 C & A).

Stamens and pistil. The thecae (Fig. 85 D) and connective appendages are more or less of the same length in the tetraploids and hexaploids, i.e. they are generally longer than in the diploids. Pollen diameter is of greater use in separating ploidy levels (Fig. 85 E). There is a good deal of overlapping, especially between tetraploids and hexaploids, but plants with a pollen diameter of less than  $16\mu$  are all diploids, and plants with a diameter exceeding  $18\mu$  are hexaploids. In tetraploids the diameter of the pollen grains varies between  $19$  and  $16\mu$ . Pollen size is thus a fairly good character in determining the ploidy level of herbarium specimens. Diploids at least can generally be distinguished from polyploids with appreciable certainty.

The style branches are of about the same size in diploids and tetraploids, and slightly longer in hexaploids (Fig. 85 F), though overlapping is great.

Fruit. No material from hexaploids was available.

In tetraploids achenes are often longer than in diploids (Fig. 85 G). But the length/breadth ratio is exactly the same. Only slight differences exist in the breadth of the achene ridges.

The similarities and differences in morphological characters within the entire material are summarized in Table 8.

Discussion. In most morphological characters there seems to be a distinct dissimilarity between the diploids on the one hand, and the tetraploids and hexaploids on the other. Many of these characters are of a quantitative nature, i.e. the respective structures are larger in the polyploids, though the opposite is true in some cases, at least when comparing hexaploids and tetraploids, e.g. in shoot length and corolla length. Other morphological dissimilarities are of a more qualitative nature, e.g. degree of branch rigidity, plants with more or less pendent branches being much more usual among tetraploids and hexaploids than among diploids. Another qualitative character, viz. corolla and phyllary colour, also shows some disparity in the material. Red corollas and phyllaries with a touch of red are frequently observed in the diploids, less often in the polyploids. Even the stems may have a reddish tinge, and this is more frequent in the diploids than in the other ploidy levels.

Another aspect of the morphological differences between diploids and tetraploids (the hexaploid material is too limited to allow of definite conclusions) is the magnitude of the range of variation. In the cases illustrated in Figs. 83--85 the tetraploids have the widest variation in 6 cases, the diploids in 7 cases, and in 4 cases they are alike. However, as the tetraploids are few in number and represent a much smaller number of populations than the diploids, the range of variation obtained for them is probably smaller than if the material had been more extensive. This deduction is confirmed by the fact that the range of variation as seen in herbarium material is actually much wider in tetraploids than in diploids.

In view of the results from both the cytological and morphological investigations, it seems rather probable that tetraploid A. santonicum is at least not an autopolyploid, but as the diploids and tetraploids are so similar in many respects the presumed allopolyploidy is probably segmental rather than total. The frequent formation of one or two multivalents apart from the usual bivalents in meiosis also points to this. It is more difficult to draw conclusions about the nature of the hexaploids as no meiotic investigation was undertaken. The two polyploid levels resemble each other in most characters. It is quite possible that the high polyploids are autoallohexaploids formed, for instance, from the tetraploids by the union



of one unreduced and one reduced gamete. As the meiosis is rather irregular in tetraploids, the occasional formation of unreduced gametes does not seem improbable.

In the author's opinion the best solution would be to treat the diploids and polyploids as two separate taxa. These two taxa and the two ploidy levels within one taxon would be reproductively isolated from each other as the immediate crossing products, being triploid or pentaploid, would be sterile. According to Löve (1964 a, b) the essential thing in such cases is the reproductive isolation, and such cytotypes should therefore be regarded as good species. Grant (1971 pp. 30--31) is also inclined to treat such cytotypes as species, biological species according to his definition. Other authors take a more practical approach, for example Yurtsey & Zhukova (1968) who state that different polyploid populations should be described as new species only when there are correlated characters on which at least the overwhelming majority of the individuals can be identified. The present author inclines more towards this view. Because of the diagnostic difficulties it would be quite impracticable to place the tetraploids and hexaploids of A. santonicum in two taxa. A similar view, which leads to tetraploids and hexaploids being placed together as one taxon, has been expressed a number of times by other authors in connection with other material (see Weinmarch 1971 on Hierochloë odorata ssp. odorata, for instance).

With respect to according the two proposed taxa (2x and 4x/6x, respectively) species or subspecies rank it seemed advisable to study a great deal more material as well as the exact geographical distribution of the taxa. As a first step in this direction pollen size was investigated in the available herbarium material containing mature pollen (169 specimens), as this is the best diagnostic character for determining ploidy level. Two frequency polygons were constructed showing 1) the frequency of individuals with a given pollen diameter, and 2) the frequency of localities with a given mean pollen diameter (Fig. 86). In both cases there was a distinct plunge in the graph at 8.2 scale units, corresponding to 20.5  $\mu$ . According to the previous investigation on cultivated material this plunge is equivalent to the dividing line between diploids and polyploids.

Consequently, there was no great difficulty in separating the diploids from the rest of the herbarium material. A later investigation on other morphological details confirmed the preliminary

results. It seemed that diploids only occur in Austria and Czechoslovakia, and polyploids only in eastern Roumania, Bulgaria, Greece and the USSR. In Hungary and western Roumania diploids and polyploids grow together in many localities, in others only one ploidy level is found (Fig. 112). In many of these Hungarian and Roumanian localities the ploidy level of the plants is very difficult to determine on morphology alone (apart from pollen size), owing to great morphological similarity. The plants seem to be intermediate between the Austrian diploids and the polyploids from the east. Two explanations of this seem possible: 1) That it is a case of introgression, perhaps via unreduced gametes of the diploids; cases of hybridization and introgression across different ploidy levels have previously been described, e.g. between diploid Leopoldia comosa and tetraploid L. weissii (Beptzer 1972), and between octoploid and decaploid Chrysanthemum shiwogiku (Shimotomai et al. 1968). 2) Natural allopolyploids often vary in the direction of one or both of the parental diploids, as they are likely to segregate occasionally for the parental characters especially if they are segmental allopolyploids. If genes determining certain morphological characters are linked with genes for viability (M-V linkage, Grant 1967), selection for the viability genes having an optimum in the environment of one of the diploid parents would have the same effect in that particular environment as introgression.

In view of the relatively large region with intermediate types that are difficult to determine without counting the chromosome number or measuring the pollen, the best taxonomic treatment in the author's opinion is to accord the two taxa (2x and 4x/6x, respectively) subspecies rank. Of these two subspecies, the diploid subspecies probably has large parts of its genome in common with at least one of the genomes in the polyploid, and within the polyploid subspecies, the hexaploids quite possibly have more than one genome in common with the tetraploids.



## GERMINATION AND TOLERANCE TO SALINITY

### SEEDLING DEVELOPMENT

When exposed to moisture the pericarp swells and a thick mucilaginous sheath develops around the achene (most pronounced in Artemisia maritima, least in A. vallesiaca). After a few days the pericarp bursts and the radicle emerges. The hypocotyl emerges 1--2 days later (under greenhouse conditions). The cotyledons are bluntly elliptical to obovate in outline in all three species, the breadth/length ratio being highest in A. maritima, lowest in A. santonicum at least in the tetraploids. Diploid A. santonicum is characterized by its smaller cotyledons, those of the tetraploids being more or less of the same size as in the other species. Small cotyledons are however also found in A. maritima forms from Öland--Gotland (Figs. 87, 88).

In A. maritima the cotyledons are more distinctly connate than in the other taxa. In all three species the cotyledons are green and wholly devoid of vestiture. Certain differences in texture exist, however, the cotyledons in A. maritima being very thick and almost succulent with a crystalline-papillose surface, while in A. vallesiaca the cotyledons are thin and delicately papillose. A. santonicum is intermediate, though most like A. maritima.

The first two leaves are opposite and more or less oblanceolate, in A. maritima and A. santonicum almost spatulate, in A. vallesiaca very narrow and almost linear; in all cases the apex is acute. Vestiture is usually sparse or lacking. As these leaves differ from all subsequently appearing leaves in that they are rarely divided, I have chosen to call them "primary leaves" (though this term is sometimes used for cotyledons). All leaves developing after the primary leaves are alternate and more or less pinnatisect and pubescent. The first of these "secondary" leaves usually has three or five segments in A. santonicum and A. maritima (Figs. 87 C, F, 88 D), and five or seven segments in A. vallesiaca (Fig. 87 I). The second leaf has five or

seven, and seven or nine segments, respectively, after which the degree of segmentation increases successively.

The whole process of germination and seedling development takes considerably less time in A. santonicum than in the other two species (Figs. 90, 91; cf. the flowering process, p. 44).

## THE EFFECT OF SODIUM CHLORIDE ON GERMINATION AND GROWTH

As two of the species in this investigation (A. maritima and A. santonicum) grow in salt-marshes and other habitats with an excess of sodium salts, especially sodium chloride, in the soil and soil water, it is of some interest to study the effect of different concentrations of salts on the physiology of these species. A number of investigations on this matter have previously been carried out on halophytes (Poma 1922, Taylor 1939, Chapman 1942, Jacquet 1949, Turner 1956), some including A. maritima. At least as regards A. maritima they have not been on a large scale with samples from different parts of the area of distribution. The present investigation on the effect of sodium chloride on germination and growth comprises four different populations of A. maritima and one of A. santonicum. A thorough investigation should, of course, have included other important physiological processes such as transpiration, respiration, and control of osmotic pressure, but this was considered to be outside the scope of this paper.

### Material Investigated

Achenes were collected from the following localities and used in the investigation (Fig. 89):

- A. Artemisia santonicum (2n=18) from Palàrikovo (Czechoslovakia)
- B. A. maritima from Bunkeflo, Skåne (Sweden)
- C. " " from Södviken, Öland (Sweden)
- D. " " from Styrsö, Bohuslän (Sweden)
- E. " " from Föhr, Nordfriesische Inseln (Germany)



### Germination

Germination globes were used, which were filled with 0 %, 0.05 %, 0.1 %, 0.2 %, 0.5 %, 1 %, 1.5 % and 2 % solutions of sodium chloride respectively, two globes of each solution. 50 achenes were sown on the filter paper in each germination globe, and the globes were placed in a greenhouse. Loss of water through evaporation was compensated for by adding distilled water daily so that a given level was kept in the globes. The experiment was controlled every day for five weeks, and the percentage of germinated achenes was noted, later also the growth of the radicle and hypocotyl.

Two series of investigation were carried out during two consecutive years, the mean values for one year being recorded here (Fig. 80). In the diagrams the number of achenes (mean values) where the radicle emerged is shown as well as the number of those where both radicle and hypocotyl emerged. The values for the latter are often lower as some achenes died soon after the emergence of the radicle. Only the achenes in which both radicle and hypocotyl emerged are considered to have germinated successfully.

It is to be noted that in each case the duration of the germination process is shorter than if pots filled with soil had been used, or in nature (in the experiment the achenes are subjected to a high humidity). The time values obtained are of most value when compared with one another.

Results. From the results of the experiment it is evident that achenes from all the populations tested germinate best under freshwater conditions. Under such conditions germination frequency generally amounts to about 90 %. In slightly saline water (up to 0.1 % NaCl) there is usually no serious decrease in germination frequency, however, though the actual rate of germination may be somewhat retarded. Achenes of A. santonicum will germinate within a short time even in higher concentrations of salt, and with fairly high frequencies too in solutions with up to 0.5 % NaCl. The same observations apply to A. maritima from Skåne (B), though germination as a whole is slower, even under freshwater conditions. On the other hand, even a concentration of 0.2 % NaCl has a decided effect on the onset of germination in the material from Öland (D), and also on the final germination frequency in the material from Bohuslän (E) and Nordfriesland (F). 1 % NaCl will cause a very pronounced decrease in germination frequency in most of the populations, above all in A. maritima. In concentrations higher than 1 % no achenes from either

population germinated. Not even the preliminary swelling of the seed was observed.

### Growth of Seedlings

In the seedlings that developed during the germination experiment, the growth of the radicle and hypocotyl was studied as well as the onset of development of the primary leaves and the first secondary leaf (Fig. 91).

Optimal development was shown to take place in very low concentrations of salt. In *A. sativum* in a solution of 0.1 % NaCl, in *A. gerardii* in 0-0.1 %, within the experimental period (8 weeks) the primary leaves developed in concentrations up to 0.8 % (---1 %) NaCl, whereas in the populations from Oland and Bornholm (0.2 % NaCl). In *A. sativum* the first secondary leaf appeared when concentrations up to 0.1 % were used, for *A. gerardii* the maximum being 0.05 %.

In concentrations as low as 0.1 % NaCl there were some examples stunted radicles in the germinated material from Ekse. In the rest of the germinating material this phenomenon did not appear until concentrations of 0.8 %. In 1 % concentrations the radicle did not develop normally in any material at all, and the hypocotyl and cotyledons were also more or less stunted. These deformed seedlings eventually died without developing further.

In order to test the tolerance to salinity of older seedlings the following experiment was carried out. Achenes from localities A--E were sown in 200 mesh sieves (vermiculite) on two occasions, at an interval of four weeks. The seedlings were watered with a weak nutrient solution containing all essential elements (a 1 % aqueous solution of a fertilizer containing: N 12 %,  $H_2PO_4$  12 %,  $K_2O$  18 %, Mg 0.4 %, per 100 mg: S corresponding to 800 g  $Mg_2P_2O_7$ , Mn corresponding to 280 g  $MnSO_4$ , Cu corresponding to 140 g  $CuSO_4$ , Zn corresponding to 90 g  $ZnSO_4$ , Co corresponding to 2.5 g  $CoSO_4$ ).

When the seedlings were 8 and 4 weeks old, respectively, they were transplanted into vermiculite-filled pots with drainage holes, three seedlings of the same stage per pot. The pots were watered twice a day with a nutrient solution to which NaCl in the following concentrations was added: 0 %, 0.01 %, 0.1 %, 0.2 %, 0.5 %, 1 %, 1.5 %, 2 %, 3 %, 4 %, 5 %, 6 %, 7 %, 8 %, 9 %, 10 %, 15 %, 20 %, 25 %, 30 %, 35 %, 40 %, 45 %, 50 %, 55 %, 60 %, 65 %, 70 %, 75 %, 80 %, 85 %, 90 %, 95 %, 100 %.



2 %, 3 % and 5 % (two pots/concentration). The slop-culture technique was employed (cf. Bonner & Galston 1958 pp. 51--52). There was probably some accumulation of salts in the pots due to evaporation, but most of these accumulated salts were presumably washed out with the large amounts of nutrient solution added twice a day.

The seedlings were observed for five weeks. Shoot measurements were made continually (Fig. 92), and the roots were measured at the beginning and end of the experiment (Fig. 93). The leaves were measured on the older seedlings only, at the end of the experiment, when leaf length, lamina breadth (Fig. 94) and segment breadth (Fig. 95) were noted. The mean values of the measurements were plotted on graphs. Some of the younger seedlings of C, D and E died immediately after transplantation and are therefore not represented.

In the younger seedlings (4 weeks old at time of transplanting) growth was optimal in nutrient solution containing no NaCl at all. Tolerance was also shown to NaCl solutions (though growth was retarded), up to about 1.5 % NaCl (in A. maritima from Nordfriesland up to 2 %). In higher concentrations the seedlings began to wilt, or even died.

The older seedlings (8 weeks old at time of transplanting) proved more tolerant to saline conditions and in most cases also showed an optimal development in weak concentrations of NaCl (Fig. 96). Thus, for A. santonicum the optimal measurements for shoot length, root length and leaf size were noted at concentrations of 0.1--0.2 % NaCl, for A. maritima from Skåne and Bohuslän at 0--0.2 %, for the same species from Nordfriesland at 0--0.1 % and from Öland at 0--0.05 %. The breadth of the leaf segments was in most cases greatest at very low concentrations (0--0.05 % NaCl), except in the case of Nordfriesland (0.2 %).

At concentrations of 1.0--1.5 % NaCl growth was mostly retarded, and at 2 % the seedlings began to wilt after a time (especially B), except in the case of E (Nordfriesland) the seedlings of which seemed to tolerate even such a high concentration. At still higher concentrations all seedlings began to wilt after a few weeks, and in some cases died.

## Other Aspects

Pubescence. The degree of pubescence on stem and leaves of 13-week-old seedlings grown for five weeks in sodium chloride solutions of different concentrations was alike at concentrations between 0 and 0.5 % NaCl, but a marked increase was evident at 1 %. At higher concentrations the seedlings were densely covered with a greyish-white to white pubescence.

Stomata. On 13-week-old seedlings grown for five weeks in a nutrient solution without and with 1 % NaCl, respectively, the length of the guard cells of the stomata on two of the youngest, but fully-developed, leaves was measured. 20 stomata on each leaf were measured and the mean value for each seedling calculated (Table 9).

It was shown that for seedlings from identical localities those grown under saline conditions had much smaller stomata than those grown in nutrient solution without NaCl. This can be compared with the fact that within the same species (A. maritima, B--E) the stomata of plants from more saline habitats (D and E) are smaller than in plants from brackish habitats (B and C), measured after the plants had been grown under uniform conditions of cultivation.

## Conclusions

Germination. The results of the investigation agree well with those found in earlier studies of other halophytes. Artemisia santonicum and A. maritima germinate best under freshwater conditions, as do the majority of halophytes, such as species of Salicornia, Suaeda, Halimione, Spergularia, Aster and Juncus, according to e.g. Chapman (1942), Jacquet (1949) and Turner (1956). A concentration as low as 1 % NaCl will cause a serious decrease in germination frequency in most of the plants investigated including the Artemisia species, except in Salicornia which tolerates extremely high degrees of salinity (greater than 10 %).

The onset of germination is also affected by moderately high concentrations of salt, as shown by Montfort (1927) for Aster tripolium and by the present author for the two Artemisia species: the onset of germination is generally delayed by a number of days or even by



weeks.

If the Artemisia species are compared, it can be concluded that A. santonicum is less affected by high degrees of salinity than A. maritima, especially as regards the onset of and rate of germination.

As regards intraspecific conditions, there seems to be some variation in tolerance to salinity of the germination process within A. maritima, but this variation is hardly correlated with the salinity of the original habitats (cf. Table 11).

The reduction in salt concentration needed to ensure the successful germination of halophytes in nature occurs in northern and central Europe in the springtime, when the increase in moisture will dilute the salts in the soil water. The seeds of most halophytes in the area germinate during this period.

Growth of seedlings. Earlier investigations have shown that in most halophytes the seedlings tolerate salinity better with age. The onset of germination and the earliest stages of seedling growth seem in fact to be a crucial period in the life of a halophyte. In older stages there is usually even a certain optimum concentration of salts. In Aster tripolium this was established as being between 0 and 0.39 % NaCl and for Salicornia stricta about 2.5 % NaCl (Montfort & Brandrup 1927, 1928). In Suaeda novae-zelandiae the young seedlings showed an optimal growth at a concentration of 1 % NaCl, older plants (six months) at 1--3 % NaCl.

The results of the present investigation on Artemisia maritima and A. santonicum agree well with these observations. Table 10 shows the NaCl concentrations giving the optimal development of seedlings at three stages. The numbers within parentheses represent the salt concentrations at which growth wholly stagnates.

Under saline conditions the very young seedlings of A. santonicum develop more rapidly than those of A. maritima. This is probably because the aridity of the habitats of A. santonicum require the young seedlings to develop rapidly even in high salinities, older seedlings being more drought resistant (cf. the rapid germination and the short flowering period of the species).

Within A. maritima the differences between populations of different geographical origin are slight. The older seedling material originating from the most brackish habitat (Öland) is slightly less tolerant to salinity than the material from the more saline habitats (cf. Tables 10 & 11), otherwise there seems to be no correlation between salt tolerance and the salinity of the original habitat.

Other aspects. The rate of transpiration of halophytes in their natural environments seems to be about the same as for glycophytes (using as a basis the time the plant takes to transpire its total weight of water, cf. Schratz 1937, Uphof 1941), in spite of the fact that halophytes usually have much lower stomata frequencies (less than 200 per sq. mm) than glycophytes (more than 100, often around 200--300 per sq. mm according to Delf 1911). Artemisia maritima falls fairly well into line with other halophytes in this respect (80--100 stomata per sq. mm on leaves).

A radical increase in salt concentration will however reduce the rate of transpiration in halophytes, too. To some extent this is expressed in A. maritima and A. santonicum through the reduced values for stomatal size and total leaf surface with increased salinity. Thus the optimum of segment breadth occurs at lower concentrations of salt than optimal growth in general.

Many authors have pointed to the presence of a number of xerophytic features in the morphological characters of halophytes. This phenomenon perhaps is an expression of the conditions of physiological drought under which these plants usually live, caused by the interference of the high salt concentrations with the absorption of water by the roots (Good 1964). For instance, Eijk (1939) and Arnold (1955) have proved the existence of a relationship between the salinity of the soil and the degree of succulence in many halophytes. Such a relationship is not evident in Artemisia species of the maritima complex, except for a tendency towards more fleshy leaves (especially cotyledons) in A. maritima as compared with the closely related A. vallesiaca (glycophyte).



## CROSSING EXPERIMENTS

### METHODS. SELF-STERILITY

To test the self-fertility of the three species (Artemisia maritima, A. vallesiaca and A. santonicum) a synflorescence on each plant to be used in crosses was isolated in an isolation bag while in bud. The bags were then shaken at intervals in order to spread the pollen effectively within the synflorescence. In no case was there any fruit-setting, which indicates total or at least a very high degree of self-sterility.

All subsequent crosses could therefore be performed by simply placing together one young synflorescence on each of the two plants to be crossed in an isolation bag, which was then shaken repeatedly to procure effective pollen distribution.

### CROSSING EXPERIMENTS BETWEEN SPECIES

There is one practical difficulty to be considered when crossing experiments between species are to be carried out, i.e. difference in flowering period. A great deal of the A. maritima material has already ceased flowering by the time A. vallesiaca and A. santonicum are in full bloom. However many attempts to cross the three species have been made in all directions. No fruit-setting was ever obtained.

## CROSSING EXPERIMENTS WITHIN SPECIES

Material

Crosses were performed on plants of A. santonicum and A. maritima cultivated in the open or in the greenhouse. The crosses within A. santonicum were performed between the different ploidy levels. No fruit-setting was ever obtained. The possibility of hybridization between two ploidy levels in nature should not be excluded, however. As was mentioned previously, a number of cases of hybridization across ploidy levels are known, and the morphology of the diploids and tetraploids of A. santonicum growing together in some Hungarian and Roumanian localities suggests, if it does not prove, the presence of introgressive hybridization. Hybridization could perhaps be explained by the occasional union of unreduced gametes from the diploids with gametes from the tetraploids, rather than by the direct union of normal gametes from the two ploidy levels, in which case the hybrids would be triploid and almost certainly sterile.

Within A. maritima crosses were mainly performed between populations geographically isolated from each other and/or with dissimilarities in morphological characters, as established in the investigation on intraspecific variation. The populations originated from the following areas: Skåne, Halland, Bohuslän, Öland/Gotland (all Sweden), north-eastern and south-western Jylland (Denmark), Nordfriesland, Ostfriesland (both Germany), north-western France, eastern and western England, and Artern (central Germany). Crosses were performed in all directions, with the following exceptions: populations from Jylland were only crossed with each other and with material from Sweden and Artern, the French and English populations were only crossed with each other and with material from Skåne and Ostfriesland, and the population from Artern was only crossed with material from Skåne, Jylland, Nordfriesland and Ostfriesland. Apart from these inter-population crosses, some crosses within populations have been carried out, viz., between plants with different chromosome numbers, e.g.  $2n=52 \times 2n=54$ .

A number of factors contribute to make the performance of



crossing tests within A. maritima problematic and the results difficult to interpret. 1) Plants from different areas flower at different periods. This is especially apparent in the material from Öland and Gotland (early-flowering) and Artern (late-flowering) as compared with most of the other populations. 2) Many of the plants used in crosses were aneuploid or aneusomatic (the euploid material was too limited to be used in all crossing combinations), and they frequently had reduced fertility on both the male and female sides. 3) The crossing technique itself (use of isolation bags) probably had a negative effect on fruit-setting, which was often extremely low. 4) As the number of achenes obtained often was so low, it was difficult to draw definite conclusions from the values obtained for germination frequencies. 5) As regards development and vitality it has been previously established that the cytologic conditions behind aneuploidy and aneusomaty have a negative effect, and crossing products with aberrant chromosome numbers are naturally affected by this condition besides by the disharmonious interactions of the parent genomes.

#### Fruit-setting After Crossing and Germination of Achenes Obtained

If the number of achenes obtained after each cross (Table 13) is compared with the fact that each synflorescence used in the crosses usually contains between 250 and 1000 flowers, it can be seen that fruit-setting is very low in the whole of the material (cf. fruit-setting in parent plants: usually 60--80 % in euploids, 20--50 % in aberrants), probably largely due to unfavourable external conditions, e.g. the high humidity in the isolation bags. Therefore the amount of fruit-setting after crossing is a rather unreliable measure of the degree of cross-compatibility between different populations. Sometimes fruit-setting failed after repeated attempts, even in cases where it would certainly have been expected. In other cases one of the reciprocal crosses was successful but not the other (Table 12).

The germination tests on the hybrid achenes are less sensitive to external conditions. Such tests also appear to be fairly reliable as a measure of reproductive isolation, at least judging from preliminary deductions from morphology and degree of geogra-

phical isolation. Two groups can be discerned in the material. The first group comprises crosses between populations from Skåne, Jylland, Nordfriesland, Ostfriesland, France and England. Germination frequencies in this group amounted to between 30 and 85 % (usually c. 50--80 %), the magnitude of the value apparently not being correlated with the condition of euploidy, aneuploidy or aneusomaty. These values can be compared with the germination frequencies obtained in spontaneous material, generally about 80 % (cf. Fig. 90). In most of the crosses within the group the hybrid achenes germinated within a fairly short time (one to two weeks, as in spontaneous material), except in some crosses involving English material, where the period of germination was longer, more than three weeks.

The second group consists of crosses between populations from Bohuslän, Halland, Öland and Gotland. The germination frequencies were mostly low or nil (usually 0--20 %, mean value 13 %), even in crosses between euploids. Moreover, the time lapse between sowing and germination was often long in crosses between the two subgroups Bohuslän--Halland and Öland--Gotland, more than two weeks (in one case even three months). Crosses between the populations from Bohuslän and Halland had higher rates of germination, viz., between one and two weeks as in spontaneous material.

Crosses between the two main groups of populations also had very low germination frequencies, usually 0--25 % (mean value 12 %), and the lapse of time before germination took place varied but was often more than two or three weeks.

The only cross ever succeeding with material from Artern as one parent, viz., with material from Ostfriesland as the paternal parent (both parents euploid), yielded only five achenes, of which only three germinated after more than three weeks.

#### Development and Vitality of Hybrid Plants

In most crosses the hybrid plants developed normally during the first year, and it was not until the second year, usually the year of the first flowering period, that differences in the material became apparent (Table 14). The hybrids within the group of populations from Skåne, Jylland, Nordfriesland, Ostfriesland, France and England usually developed flowering shoots with a frequency of between 40



and 60 % (mean value 52 %), which can be compared with the values in spontaneous material: 55--65 % (cf. Fig. 4). The number of flowering plants varied slightly during the following years, but this was probably caused by variations in environment, e.g. climatic conditions. Some of the plants died during the course of the investigation, usually those which had not flowered. The total mortality, calculated at the end of the period of investigation, often amounted to only 10--20 %, and in some crosses no plants at all died (mean value 17 %).

In the rest of the material variation was greater. The onset of flowering was often delayed for one or two years, as compared with the crosses discussed in the preceding section. Two crosses never developed flowering shoots, viz., one involving plants from Bohuslän, and one involving plants from Gotland, both with a population from Skåne as the other parent. In other cases heterosis was displayed, with as many as 70--75 % of the hybrid plants flowering on vigorous shoots. The most distinct example of this heterosis was the only cross between populations from Bohuslän (female parent) and Gotland (male parent) ever to develop  $F_1$  plants (no. 47 x 5). Other hybrids with populations from Bohuslän, Halland or Öland/Gotland as parents showed rather low flowering frequencies (20--25 %), except the Bohuslän x Halland cross and its reciprocal cross: 45--60 % of these hybrids eventually flowered. The mean value for crosses within the group Bohuslän--Halland--Öland--Gotland was 59 %, and for crosses between this group and the rest of the material 28 %.

The mortality within the group of crosses between populations from Bohuslän, Halland, Öland and Gotland was often quite high, between 30 and 40 % (mean value 35 %). In crosses between this group and the rest of the material the mortality varied, but was often nil (mean value 28 %).

In the Artern x Ostfriesland cross two out of three plants flowered during the first year.

## Morphology of Hybrid Plants

The majority of the hybrids that developed flowering shoots were more or less intermediate between the parents in most morphological characters and also as vigorous as the parents. However, in some crosses many or most of the hybrid plants resembled one parent more than the other in at least some characters. In many crosses some of the daughter plants and in a few crosses the majority of them exceeded both parents in one or more characters. Only seldom were the majority of the hybrids in general appearance more vigorous than the parents. As was mentioned before, this heterosis was especially apparent in a cross between a population from Bohuslän and one from Gotland (no. 47 x 5) but was also distinguishing for crosses between western England and Skåne (no. 150 x 16), and between eastern England and Ostfriesland (no. 155 x 77). Still more rare was the occurrence of weak, malformed hybrids. Such plants were observed among the products of a cross between material from Bohuslän and Ostfriesland (no. 89 x 77) and of the above-mentioned cross no. 47 x 5.

Leaves. Most of the hybrids were intermediate between the parents in all leaf characters, such as lamina length (Fig. 97 A, C), lamina length/breadth ratio (Fig. 97 E, F), segmentation, segment breadth (Fig. 97 H, I) and segment shape. In many crosses a few of the hybrid plants were more like one of the parents or even lay outside the range of both parents in one or two characters (Fig. 97 A, E, F, H, I). Only rarely did the majority of the crossing products lie outside the range of the parents in a particular character, e.g. lamina length/breadth ratio (Fig. 97 D) and degree of segmentation (Fig. 97 G), or they were more like the one parent, e.g. in lamina length (Fig. 97 B), degree of segmentation and segment shape.

In cases where reciprocal hybrids existed no differences between the products of the two crosses were observed except as regards absolute measurements in the cases of heterosis, and a few ratio characters, e.g. degree of segmentation and segment shape in crosses no. 5 x 47 (Gotland x Bohuslän) and no. 47 x 5 where the crossing products were most like the maternal parent in both crosses.

Shoot morphology. The crossing products were mostly intermediate in characters such as shoot length, pubescence, suffrutescence and branch rigidity. In most crosses some plants more closely resembled one parent or lay outside the range of both parents. More seldom the majority of the hybrid plants were most like one of the parents,



e.g. in pubescence (cross no. 14 x 47, Skåne x Bohuslän, was as densely pubescent as no. 47), suffrutescence (Fig. 98 C), branch rigidity (Fig. 98 E) or position of capitula (Fig. 98 G). Or they were unlike both parents, e.g. in shoot length (Fig. 98 I). No reciprocal differences were detected, except in cases of heterosis.

Capitula. In some cases the majority of the products of a cross were not wholly intermediate but more like one of the parents in one or two characters. Thus, the hybrids no. 5 x 47 (Gotland x Bohuslän) and the reciprocal hybrids had phyllaries mostly as narrow as no. 5, and likewise, the phyllaries of no. 59 x 19 (N.E. Jylland x Skåne) were most like those of no. 19 (Fig. 99 A, B). In the cross no. 5 x 47 (and no. 47 x 5) the daughter individuals also had approximately the same number of florets per head as the parent population no. 5 (Fig. 99 C).

Floret. Many of the differences in floral characters between the parental populations are subtle, and therefore it is rather difficult to observe any special pattern in the variation of the crossing products. However, where the parent plants were sufficiently dissimilar it was apparent that the hybrids were more or less intermediate in corolla (Fig. 99 D), stamen and pistil (Fig. 99 E--G) characters with occasional examples of individuals being more like or exceeding the parents. In rare instances the majority of the crossing products resembled one of the parents. There were no distinct differences between reciprocal hybrids in any floral character.

Fruit. Achenes obtained after open pollination of the hybrids were measured. In many cases the achenes were intermediate in size compared with those of the parents (Fig. 99 J). In other rare cases the achenes of the crossing products were mostly of the same size as (partly exceeding) those of one of the parents (Fig. 99 H), or the majority of the hybrids even exceeded both parents (Fig. 99 I). No achenes from both hybrid types of a reciprocal crossing were available, so it was not possible to establish differences in this respect.

## Meiosis and Pollen Fertility in Hybrid Plants

Studies on meiosis in the hybrids were performed on only a limited amount of material. Samples were taken from crosses between parents representing different levels of morphological diversity and geographical isolation.

Disturbances were found in all hybrid plants investigated but in varying degrees. The aberrations were of all types found in the parent material, i.e. laggards and bridges at anaphase I and II, formation of micronuclei, giant nuclei and other tetrad nuclei of varying size and number, formation of twin pollen grains etc. In many cases the disturbance frequency was much higher in the hybrid than in either parent, e.g. the frequency of bridge and fragment formation. The latter was the case in e.g. crosses between Gotland and Skåne (total disturbance frequency 15--20 %), and some crosses between Gotland and Bohuslän. In other cases the degree of aberrant meiosis was about the same or only slightly higher in the hybrid than in the parents, e.g. 5--10 % disturbed divisions in a cross between a population from north-eastern Jylland and a population from Skåne. The cross no. 47 x 5 (Bohuslän x Gotland), which displayed heterosis in morphological characters, apparently had a regular first division but an irregular second division. The tetrad cells were of somewhat variable size but seldom exceeded four in number. The two parents in this case differed in disturbance frequency: the parent from Bohuslän with  $2n=52$  had about 5 % disturbed divisions, and the parent from Gotland with  $2n=54$  had an apparently regular meiosis.

The higher frequency of bridge and fragment formation in many hybrids between populations from different regions points to a higher degree of structural heterozygosity, probably for inversions, in such hybrids.

Pollen stainability values obtained for the hybrids were in many cases lower by more than 10 % than the frequencies of regular meiotic divisions, just as in parents. Part of the reduction in pollen fertility is therefore probably caused by genic and cryptic differences rather than by major structural rearrangements. The variation in pollen stainability was often very wide in the hybrid generation, with values in many cases both much lower and much higher than for the parents. To judge from the often very low pollen fertility values many of the hybrid plants may have originated from unbalanced gametes formed by the parents. Such gametes are probably occasionally functionable, which is indicated by the cytologic conditions, degree of fer-



tility and viability of the spontaneous plants as discussed earlier in this paper. In many cases, however, the pollen stainability values for the hybrid material as a whole indicated a general reduction in fertility, and the mean value was often lower than in one or both of the parents. In most of the crosses between populations not originating from Gotland, Bohuslän or Halland the mean values for the pollen stainability in the hybrids usually amounted to 70--90 %, i.e. not lower than or somewhat lower than in the parents. Crosses between populations from Bohuslän and Halland showed approximately the same values, but other crosses involving these and the populations from Gotland often had lower values, at least lower than the parents. One exception was the heterotic hybrid no. 47 x 5 (Bohuslän x Gotland), which had as much as 88 % stainable pollen (mean value).

The pollen fertility values were not exactly correlated with the frequencies of germinated hybrid achenes as listed in Table 13, but there were not many exceptions. One exception was hybrid no. 47 x 5 (Bohuslän x Gotland) that displayed heterosis and had 88 % stainable pollen: only 16.7 % of the original achenes had germinated. Otherwise it is fairly evident that hybrids with very low pollen fertility values also had low germination values, and that hybrids originating from achenes with a proportionately high germination frequency generally had more than 80 % stainable pollen.

Pollen stainability values for crosses between populations of different geographical origin are listed in Table 15, but it must be remembered that these values are not directly comparable but must be seen in relation to the pollen stainability values and cytologic conditions in the respective parents, as discussed above.

### Number of Chromosomes in Hybrid Plants

respectively), and aneusomatics 32 % (35 % and 29 %, respectively). 24 % of the crosses performed were between euploid plants. The percentage of euploids amongst the total number of hybrid plants counted amounted to 55 %. Of the remaining 45 %, c. 31 % were aneuploids and c. 14 % aneusomatics (it is remarkable that the proportions of aneuploidy and aneusomaty in this material containing 55 % euploids are exactly the same as in a wild population with the same euploidy frequency, viz., the spontaneous material from western France, cf. Table 2). The actual chromosome numbers obtained in different crossing combinations are summed up in Table 16.

It can be seen that all crosses between euploids result in euploid offspring. This is not unexpected as meiosis in euploids with few exceptions has been shown to be regular producing gametes with  $n=27$ . The rest of the hybrid generation, originating from other crossing combinations and probably occasionally from a union of unbalanced gametes, consists of plants with chromosome numbers ranging from 51 to 56, 53 and 54 being the most frequent.

#### Fruit-setting and Germination of Achenes Obtained After Sib-mating Within $F_1$

To produce an  $F_2$  generation the plants from an  $F_1$  family that were in flower were placed together in the greenhouse (isolated from other plants), and their synflorescences were shaken intermittently to procure an effective dispersal of pollen. Only a limited amount of  $F_2$  material has been produced as yet.

Within the group of crosses between populations from Skåne, Jylland, Nordfriesland and Ostfriesland both fruit-setting (number of achenes produced per plant) and germinating capacity of the achenes obtained showed an increase or remained unchanged in the  $F_1$  generation (Table 17) as compared with the original crosses. One cross was especially successful, viz., the cross between north-eastern Jylland and Skåne, and it also had the shortest germination period. In the group Bohuslän--Gotland there were reciprocal differences. Where the population from Bohuslän was used as maternal parent, the values for both fruit-setting (about 100 achenes per plant) and germination were higher for the  $F_1$  plants (mostly heterotic) than for the original



crosses, while in the reciprocal cross fruit-setting was much decreased in  $F_1$  but a high percentage of the few achenes obtained germinated.

In  $F_1$  plants of crosses between the two groups mentioned, fruit-setting was very limited (even lower than in the original crosses), but most of the achenes obtained germinated.

Within each  $F_2$  family the different  $F_1$  progenies showed a fairly wide variation in both germination frequency and rate of germination. It is therefore probable that the genetical basis determining germination is multifactorial, and that a recombination of factors affecting germination has occurred, resulting in achenes displaying low as well as very high or intermediate germination frequencies and germination rates.

#### Development, Morphology and Vitality of $F_2$ Plants

In all crosses, but especially in those between Bohuslän and Gotland, there were a number of the young  $F_2$  seedlings with malformed and/or stunted cotyledons and radicles, and many of them died at an early stage. In the later stages, too, different kinds of abnormalities were displayed, e.g. shortened internodes, malformed bent stems, an abnormally high number of leaves, abnormally segmented leaves, compressed synflorescences, irregular flowering, etc. Thus the one flowering plant obtained from the Gotland x Skåne cross, some from the Bohuslän x Gotland cross, and a number from the other crosses were malformed in varying degrees. Most crosses developed flowering shoots during the second year, the N.E. Jylland x Skåne cross as early as the first year on three small, undeveloped plants. The majority of the  $F_2$  families flowered to about 40--50 %, with the highest frequencies found in the Nordfriesland x Ostfriesland cross. Two crosses never flowered at all, viz., no. 88 x 101 (Gotland x Skåne) and no. 5 x 47 (Gotland x Bohuslän).

In general the  $F_2$  generation showed a much wider range of variation in morphological characters than the parental and  $F_1$  generations. Many  $F_2$  individuals were intermediate between the parents to a varying degree, but there were also "new" combinations of characters. More remarkable was the recovery of types that closely resem-

bled the original parents, a phenomenon that was especially evident in the Bohuslän x Gotland cross (no. 47 x 5). Some of these  $F_2$  plants were practically indistinguishable from one or the other of the original parents (Fig. 100). In most plant material the recovery of parent types as early as in the  $F_2$  generation is not possible unless a very large number of individuals are raised (cf. Stebbins 1950 p. 259). Some exceptions have been reported, however, e.g. crosses within the genus Apocynum (Anderson 1936). To judge from the appearance of the  $F_1$  and  $F_2$  individuals of Artemisia maritima, most morphological characters have a multifactorial genetical basis. Genetic linkage between such factors is to be expected, as in such cases each chromosome will carry genes determining the expression of several characters. Consequently correlation between groups of parental characters in the  $F_2$  generation is not surprising, and this correlation will be more evident the greater the number of factors that constitute the genetical basis of each character. Still, in view of the relative rarity in plant material of a more or less complete recovery of the parental types as early as in  $F_2$ , the genetical background is in this case perhaps still more complicated. The possibility that genes controlling the viability of the seedlings are linked with genes for different morphological characters cannot be excluded (so-called M-V linkage, cf. Grant 1967). In such a case, and under climatic conditions resembling those of the parental localities the occurrence of an abnormally high proportion of parental types even among  $F_2$  individuals is to be expected.

A tendency towards greater vitality in mature  $F_2$  plants closely resembling the parents could perhaps also be explained by the M-V linkage theory. Among  $F_2$  individuals of cross no. 47 x 5 (Bohuslän x Gotland) there were proportionately c. 4 % more parent types four years after sowing than two years previously. On the whole, the  $F_2$  plants no. 47 x 5 were very vigorous (note: the  $F_1$  generation displayed heterosis) compared with the rest of the material -- after three years only about 3 % of the mature plants had died. In other  $F_2$  families mortality was much higher, mostly between 20 and 30 %, lowest (c. 8 %) in the Nordfriesland x Ostfriesland cross.



### Pollen Fertility and Fruit-setting in $F_2$ Plants

Pollen stainability values in  $F_2$  plants covered a wide range of variation, usually from far below the parent values and the  $F_1$  mean to around 90 % or more. The genetical basis affecting fertility is evidently multifactorial, and an extensive recombination had occurred. The widest variation and also the lowest values were found in cross no. 47 x 5 (Bohuslän x Gotland, Table 18), with a mean value of c. 63 %. The pollen grains of these  $F_2$  plants varied greatly in size, with a great number of both giant and dwarf pollen grains, and also some twin pollen grains. Very often the walls were malformed or shrivelled, but most of the pollen grains had the normal number of colpi. Many of the pollen grains abnormal in size or shape stained with cotton blue but it is doubtful whether they were really functionable. However, it was evident that the meiotic divisions preceding pollen formation in many of these  $F_2$  plants had been highly irregular. In two plants the entire process of pollen formation was delayed -- the pollen grains had still not matured and the thecae had not opened even long after the stigma had withered.

The results for the Gotland x Skåne cross (no. 88 x 101) were similar (only one  $F_2$  plant existed), but in the other crosses with  $F_2$  plants the variation was less extensive (c. 30--90 %), and the mean values were higher (c. 70 % in all cases). Still, there were some examples of abnormal pollen formation in these plants, too. In three plants of the cross no. 59 x 19 (N.E. Jylland x Skåne) giant and dwarf pollen grains were observed, and in a few other plants there was also some variation in pollen size though it was not so extreme, and the pollen grains had sometimes an abnormal number of colpi. The most regular pollen formation had evidently taken place in the cross no. 69 x 76 (Nordfriesland x Ostfriesland), because abnormal pollen grains were found in only a few plants and at low frequencies.

Fruit-setting in the  $F_2$  families with plants that flowered was tested after open pollination. Considering the number of florets per plant, fruit-setting was rather low in the entire material (up to c. 25 achenes/shoot), but just as in the case of pollen fertility two classes of degree of fertility could be observed. In one class, comprising crosses between populations from Skåne and Jylland and between populations from Nordfriesland and Ostfriesland the mean frequency of fruit-setting was only slightly less than in  $F_1$ , being least in the latter cross, but the variation between  $F_2$

plants was great (cf. pollen fertility). In the other class, involving the crosses between populations from Bohuslän and Gotland, fruit-setting in  $F_2$  plants was about 35 times lower than in  $F_1$ , or to be exact, only between 1 and 10 achenes were produced per synflorescence (mean value for  $F_1$  79 achenes per synflorescence), and some plants did not set fruit at all. Moreover, many of the achenes produced were small and wrinkled and did not germinate in later germination tests.

Cross no. 47 x 5 (Bohuslän x Gotland) was distinguished in that it produced an abnormally high proportion of  $F_2$  plants closely resembling the parents in appearance, and this proportion even increased with the years. It was suggested that these plants probably had a higher vitality compared with other plants within the  $F_2$  generation. An interesting question was whether the degree of fertility also was higher in these plants than on the average. However, an investigation into this matter showed that there was absolutely no correlation between morphological appearance and degree of fertility, neither with pollen stainability nor fruit-setting, as the following figures show: for types resembling parents pollen stainability values such as 21, 40, 43, 52, 73, 76, 77 and 83 % were found, and for more or less intermediate types values such as 52, 57, 58, 67, 71 and 81 %. The  $F_2$  plants in Fig. 100 had the following pollen fertility values: B 52 %, C 43 %, D 53 %, E 67 %, F 88 % and G 52 %. Evidence of the relative independence of morphological divergence and the development of hybrid sterility has been given on a number of occasions for other plant material, e.g. for species hybrids, Galeopsis tetrahit x bifida (Müntzing 1930), and for intervarietal hybrids, Oryza sativa (Terao & Midusima 1939). In these crosses there was no correlation between morphology (as compared with parents) and fertility.

## Conclusions

1) Partial reproductive isolation is evidently prevalent in some races versus the rest of the material. There is good agreement between morphological diversity, geographical isolation, and the magnitude of the sterility barrier, as exemplified in particular by the populations from Öland and Gotland but also by the populations from



Bohuslän, Halland and possibly Årtern (the material from this locality is very limited). The morphologically and geographically close populations from Bohuslän and Halland seem to form a group of their own, with a somewhat lesser degree of reproductive isolation existing between them than between either one of them and the rest of the material.

2) The barriers between the races are expressed as A) occasional breakdowns in  $F_1$  though mainly in  $F_2$ , probably owing to disharmonious interactions between the genes of the different ecotypes; B) lowered fertility in hybrids as compared with that of the parents. Much of this reduction in fertility is obviously caused by structural hybridity, e.g. for paracentric inversions.

3) The wide range of variation in germination of  $F_2$  achenes and in fertility of  $F_2$  plants indicates that these processes probably have a multifactorial genetical basis, with extensive recombination as a result of sib-mating within the  $F_1$  generation.

4) Most primary hybrids are intermediate in morphologic characters in relation to their parents. A wide variation with occasional recoveries of types resembling original parents in  $F_2$  indicates that the genetical basis for most morphologic characters is multifactorial and that there is a high degree of genetic linkage between factors determining different characters. Some sort of M-V linkage is probably also present.

5) There is no correlation between morphological appearance and degree of fertility within the  $F_2$  generation.

## TAXONOMY, DISTRIBUTION AND HABITAT

All observations on morphological characters are based on spontaneous material. The notes on habitat and plant associations are founded mainly on Gams (1929), Wendelberger (1950), Chapman (1960) and Gillner (1965), as well as on my own field observations.

Synonymic variety names are included in the taxonomy only when the name in question has been much in use and/or has been published in standard floras or in major studies on Artemisia.

### Key to the Taxa

As all taxa vary widely as regards morphological characters, the key of necessity comprises short descriptions rather than a few simple key characters. Each specimen to be determined should always be checked against the full descriptions.

1. Stem and leaves at anthesis almost glabrous--sparsely pubescent, lower leaves soon withering and falling off.....2
- Stem and leaves at anthesis moderately--densely pubescent, lower leaves long persistent.....4
2. Phyllaries in rather close, imbricate arrangement (outer ones much smaller than inner ones), inner phyllaries subacute--acute, glabrous except for glands, glossy, herbaceous midrib region linear or tapering towards the point.....3
- Phyllaries somewhat spreading in a diffusely imbricate arrangement (outer ones  $\frac{1}{3}$ -- $\frac{1}{2}$  the size of the inner ones), inner phyllaries blunt--subacute, sparsely--moderately pubescent, surface with a dull gloss, herbaceous midrib region more or less spatulate.....A. maritima ssp. maritima
3. Branches mostly pendent; leaf segments 0.5--0.8 mm broad; inner phyllaries 1.2--1.6 mm broad; corolla 2.3--2.8 mm long; pollen grains 19--30  $\mu$  (usually 21--25  $\mu$ ) in diam. ....  
A. santonicum ssp. santonicum
- Branches mostly erect; leaf segments 0.4--0.6 mm broad; inner phyllaries 0.9--1.4 mm broad; corolla 1.9--2.4 mm long; pollen grains 14--20  $\mu$  (usually 17--20  $\mu$ ) in diam. ....  
A. santonicum ssp. patens



4. Rhizome short, strongly lignified, with many small rosette-bearing sterile shoots; branches erect; leaves 3--4-pinnatisect with crowded, 0.3--0.5 mm broad segments, mostly large pinnatisect auricles; inner phyllaries rather densely pubescent in upper half, scarious margins abruptly narrowing towards the base.....A. vallesiaca
- Rhizome rather long, mostly moderately lignified, with a moderate number of rosette-bearing sterile shoots; branches erect--pendent; leaves 2--3-pinnatisect with 0.4--1.2 mm broad segments, small entire or moderately segmented auricles or without auricles; inner phyllaries sparsely--moderately pubescent, scarious margins gradually narrowing towards the base...5
5. Stems ascending, usually 20--60 cm, moderately--strongly suffrutescent, moderately--densely pubescent; synflorescence rather lax--moderately compact, very seldom spicate, branches usually 5--10 cm long; laminae of lower cauline leaves 10--45 mm x 7--30 mm; corolla 2.5--3.2 mm long, style branches 0.6--0.9 mm long.....A. maritima ssp. maritima
- Stems decumbent--ascending, usually 5--25 cm, slightly suffrutescent, densely pubescent; synflorescence mostly dense, often spicate, branches usually 0--3 cm long; laminae of lower cauline leaves 5--18 mm x 4--13 mm; corolla 2.4--2.8(--3.0) mm long, style branches 0.4--0.7 mm long..A. maritima ssp. humifusa

# ARTEMISIA MARITIMA L.

Linnaeus 1753 p. 846. -- Original collection: without locality (LINN no. 988:20 /pinned to sheet no. 21/, lectotype).

A. salina Willdenow 1803 p. 1834 (excl. pl. Hung.). -- A. maritima L. ssp. salina (Willd.) Reichenbach 1831 p. 221. -- Original collection: Germany, Mansfeld (B, Herb. Willd. no. 15379:2, left specimen on sheet, lectotype).

A. hybrida Sagorski 1908 p. 86. -- Original collection: Germany, Artern, Oct. 1906. Leg. Sagorski (JE, lectotype).

A. maritima L.  $\gamma$ . suffruticosa Hartman 1820 p. 306. -- Original collection: without locality (UPS, Herb. Hartm., left specimen on sheet, lectotype).

A. maritima L.  $\xi$ . wallrothiana Besser 1834 p. 40. -- Description and distribution confirm the synonymy.

Illegitimate synonym: A. seriphium Wallroth 1822 p. 458 (superfluous as A. maritima L. was cited as synonym).

Invalid synonyms: A. maritima L.  $\xi$ . linnaeana Besser 1834 p. 33 (excl. pl. Dalm. et Sib.). -- A. maritima L.  $\delta$ . genuina Ledebour 1845 p. 571 (excl. pl. Taur.).

Note: The name "gallica" for a variety of A. maritima L. s. str. with erect branches and capitula is often met with in floras and on herbarium sheets. It originated due to a misunderstanding of Willdenow's A. gallica, which is a Mediterranean species. Though it has the characteristics mentioned, it is otherwise very different from A. maritima L. Rouy (1903 p. 300) suggested the name "pseudogallica" for the maritima form to make the distinction clear. However, there is no need to recognize the variety (or form) in question, as it is only one of a number of forms occurring in most populations. This also applies to "var. salina", which has also been used indiscriminately by various authors. This variety was perhaps originally founded on A. salina Willd., but Willdenow's restricted sense of the taxon has been greatly extended to comprise all forms with pendulous capitula within the area of distribution of A. maritima, especially after Koch's (1837 p. 369) insufficient description " $\gamma$ . salina Willd.: flores penduli".

The populations from Thüringen in central Germany have often been wrongly classified as being conspecific with Austro-Hungarian material now recognized as A. santonicum L. Thus Willdenow cited Germany and Hungary as the area of distribution for his species A. salina (1803), which is here typified as being synonymous with A. maritima L. on Willdenow's material from Thüringen (Mansfeld). Sagorski (1907 pp. 15, 16) described two subspecies of A. salina from Artern (Thüringen), but one of them was incorrectly founded on Neilreich's (1859) variety described from Austria (i.e. synonymous with A. santonicum L.), viz., A. maritima L.  $\beta$ . patens, and the other was founded on A. monogyna Waldst. & Kit. (also synonymous with A. santonicum L.). "A. hybrida" was used by Sagorski (1908) for forms intermediate between "ssp. patens" and "ssp. monogyna".

ILLUSTRATIONS: Figs. 102--109 (habit), 101 (distribution).



A suffrutex with a long creeping, horizontal or slightly ascending, moderately branched rhizome, c. 2--8(--10) mm in diam., usually with smooth surface. Internodes c. 10--30 mm long. A fairly rich production of sterile rosette-bearing shoots. -- Stems ascending, seldom decumbent, of very varying length, c. 5--60 cm, slightly --strongly suffrutescent, sparsely--densely pubescent (more sparsely pubescent after anthesis), sparingly--moderately branched, usually from below the middle, sometimes from the base. Branches of very varying but usually moderate length, (0--)1--10(--20) cm, usually more or less pendent (sometimes wholly pendent) but not seldom erect. -- Lower cauline leaves distinctly petioled, sometimes auricled, moderately--densely pubescent (greyish-green--white), dropping off towards fruiting stage. Laminae c. 5--45 mm x 4--30 mm, 2--3-pinnatisect, with segments c. 0.4--0.9(--1.2) mm broad, mostly more or less spatulate with a subacute--obtuse apex, sometimes linear, acutely--subacutely apiced. Leaves on sterile shoots similar but with broader and more distinctly spatulate segments. Upper cauline leaves increasingly simple, uppermost pinnatifid or entire. Stomatal cells c. 25--43  $\mu$  long (usually  $>30 \mu$ ). -- Hairs on stems, branches and leaves T-shaped with very long arms, usually two basal cells. Glands c. 40--50  $\mu$  at broadest part (top), each gland consisting of eight secreting cells in two rows and two basal cells; present on all aerial parts (except achenes). -- Synflorescence rather lax--moderately compact, seldom spicate, often more or less secund, with almost sessile--shortly stalked capitula on panicle branches of primary or secondary order (seldom spicately arranged). -- Capitula erect or pendent, elliptic--broadly ovate, c. 3--6 mm long, with peduncles c. 0--2(--4) mm long. -- Phyllaries somewhat spreading, diffusely imbricate, glandular; outer ones usually rather small, narrowly--broadly triangular (sometimes mucronate), with or without scarious margins c. 0.1--0.4 mm broad at least basally, moderately--densely pubescent; inner ones narrowly--broadly elliptic(--obovate), c. 3.0--4.5 mm x 1.0--2.2 mm, blunt, seldom subacute, with scarious margins c. 0.3--0.8 mm broad often undulate in the upper part, herbaceous midrib region often with red margins, usually spatulate and subacute--blunt, sparsely--moderately pubescent at least in upper half; upper part of scarious margins sometimes ciliate with very coarse, long hairs. -- Florets c. 3--9(--11), all hermaphrodite. Corolla c. 2.4--3.2 mm long, reddish, sometimes yellow, glandular, tubular, widening slightly in the upper part; corolla lobes 5, rather narrowly--broadly triangular, c. 0.30--0.60 mm

long. Corolla length/lobe length ratio c. 4.5--9.0. Anthers c. (0.8--1.0--1.4 mm long, acutely appendaged basally; apical appendage lanceolate, c. 0.25--0.40 mm long, subacute. Pollen grains tricolporate, c. 18--27  $\mu$  in diam. (usually  $>20\mu$ ). Style shorter or (mostly) longer than corolla tube, style branches flattened, c. (0.4--0.5--0.9 mm long. -- Achenes obovate, c. (1.5--1.8--2.8 mm x 0.7--1.4 mm, with low longitudinal ridges c. 50--100  $\mu$  broad. Style scar usually oblique, often surrounded by a more or less conspicuous bulge. -- Chromosome number  $2n=54$  (50--56).

Artemisia maritima L. ssp. maritima

Bibliography and synonymy as under the species.

ILLUSTRATIONS: Figs. 102--107.

Rhizome rather long and horizontal--slightly ascending, c. (2--3--8(--10) mm in diam., moderately--strongly lignified. -- Stems ascending, c. (15--20--60 cm, moderately--strongly suffrutescent, sparsely--densely pubescent, moderately--richly branched. Branches c. (1--5--10(--20) cm, seldom erect. -- A moderate production of sterile rosette-bearing shoots. -- Leaves (sparsely--moderately--densely pubescent. Laminae of lower cauline leaves c. 10--45 mm x 7--30 mm, with acute--subacute, seldom blunt segments c. 0.4--0.9(--1.2) mm broad. -- Synflorescence rather lax--moderately compact, very seldom spicate, seldom wholly secund, with almost sessile--shortly stalked capitula on panicle branches of primary--secondary order (very seldom spicately arranged). -- Capitula c. 3.5--6 mm long, erect or pendent. -- Inner phyllaries narrowly--broadly elliptic(--obovate), c. (3.0--3.2--4.5 mm x (1.0--1.4--2.2 mm, sparsely--moderately pubescent, scarious margins c. (0.3--0.5--0.8 mm broad. -- Florets c. 3--9(--11). Corolla c. 2.5--3.2 mm long; corolla lobes narrowly--broadly triangular, (0.30--0.35--0.60 mm x (0.25--0.30--0.55 mm. Corolla length/lobe length ratio c. 4.5--9.0. Anthers c. (0.8--1.0--1.4 mm long, apical appendage c. 0.30--0.40 mm long. Style branches c. 0.6--0.9 mm long. -- Achenes c. (1.6--1.8--2.8 mm x (0.8--0.9--1.4 mm, with ridges c. 50--100  $\mu$  broad.



DISTRIBUTION: Coasts of north-western Europe from southern Norway (only one locality near the Swedish border) to south-western France, salines near Artern and Eisleben in Thüringen, central Germany.

FLOWERING PERIOD: End of August--September(--beginning of October).

A highly variable taxon. However, it is possible to discern certain geographically and ecologically limited form series within the large area of distribution. Some of these form series are morphologically more well-defined than others. This is especially true of the form series in western Sweden and in central Germany. For reasons stated in the section on intraspecific variation, the author has chosen not to accord them taxonomic status, however.

Table 19 gives a survey of the morphological characters of the form series.

#### The West\_Swedish\_Form\_Series\_

In W. Sweden A. maritima is rare, with small populations scattered along the coast of Halland and on the islands off the coast of Bohuslän (very rarely on the mainland). All populations are more or less isolated from one another, and there is a rather long gap between the populations of Skåne and Halland. However, some of the populations in W. Sweden, especially the southernmost, have much in common with the Baltic Form Series. On the other hand, some of the populations from northern and central Halland, which have a biotope that differs somewhat from that of the populations from Bohuslän, have certain characteristics of their own that distinguish them from the latter populations.

DESCRIPTION: Rhizome of moderate length, usually slightly ascending, c. 6--8(--10) mm in diam., strongly lignified. -- Stems c. (15--30--50(--60) cm, (moderately--strongly suffrutescent, densely pubescent (greyish-white--white), moderately--richly branched. Branches c. 3--10(--15) cm, usually wholly or distally pendent, seldom erect. -- Leaves densely pubescent. Leaf segments elongate, usually distinctly spatulate, c. 0.5--0.9(--1.0) mm broad, subacute--almost blunt. -- Synflorescence rather lax--moderately compact, not seldom wholly secund, with branches of a primary or secondary order.

-- Capitula c. (4--5)5--6 mm long, often clustered in larger aggregates. -- Inner phyllaries c. (3.2--3.4)3.4--4.5 mm x 1.5--2.2 mm, moderately pubescent. -- Florets c. 5--9(--11). Corolla with broadly triangular lobes c. 0.40--0.50 mm x 0.40--0.55 mm. Corolla length/lobe length ratio c. 5.0--7.5. -- Achenes relatively broader, more convex in outline (less distinctly pyriform) than in the other form series; c. 1.8--2.6 mm x 0.9--1.4 mm, with ridges c. 50--75  $\mu$  broad.

In comparison with the populations in Bohuslän, those in Halland (at least the northern ones) often have shorter stems (c. 15--30 cm) and in some cases much simpler synflorescences (sometimes spicate). Furthermore, the phyllaries are usually shorter (c. 3.2--3.6 mm) and consequently also the capitula (c. 4--5 mm).

ILLUSTRATIONS: Fig. 102.

FLOWERING PERIOD: September.

HABITAT: The tidal range is small but seasonal variation is generally considerable in western Sweden. A. maritima is restricted to limited areas of salt-marshes on a few flat beaches and in the inner parts of bays in rocky shorelines. The salinity of the sea-water varies between 2 and 3 %.

In Halland the biotope is usually a marsh-like sea-shore meadow of moderate size. A. maritima populations occur in the lower half of Festuca rubra--Agrostis stolonifera communities. Occasionally, where grazing is intensive, species such as Leontodon autumnalis and Rumex crispus are seen together with Artemisia, or else tall grass vegetation with Festuca rubra and Agropyron repens as dominants and scattered Plantago maritima and Atriplex litoralis.

Most of the localities in Bohuslän and a few in Halland consist of very small salt-marsh areas (often only a few sq.m) surrounded by rocks. A. maritima occurs in very small populations, sometimes together with Limonium vulgare, in the central and upper geolittoral. The association formed by these two species, viz. Artemisietum maritimae, may include as subordinate species Agrostis stolonifera, Festuca rubra, Juncus gerardi, Plantago maritima and Armeria maritima, with the following additional species where the vegetation is influenced by grazing and/or fertilized by algae: Agropyron repens, Atriplex latifolia, Rumex crispus, Potentilla anserina, Leontodon autumnalis, Tripleurospermum maritimum, Senecio viscosus and Sonchus arvensis.



The Baltic Form Series

A. maritima ssp. maritima is extremely rare on the coasts of the Baltic. Only four localities have been reported from Sweden and this is verified by herbarium sheets from the beginning of this century, but the subspecies has not been refound by the present author. With increasing salinity the subspecies becomes commoner, and there are a number of localities on the Baltic coast of Germany and especially along the outlets of the Baltic Sea (the Belts and the Sound).

The difference in biotope (salinity, substrate, tidal conditions etc.) between this and the North Sea Form Series has led to the evolution of populations slightly different in morphology, but there is no distinct boundary between the two groups, the populations on the eastern coast of Jylland being intermediate.

DESCRIPTION: Rhizome fairly long and horizontal--slightly ascending, c. 4--8 mm in diam., moderately--strongly lignified. -- Stems c. (20--30--50 cm, moderately--strongly suffrutescent, moderately pubescent (greyish-green--grey), moderately--richly branched. Branches c. 5--15(--20) cm, usually pendent distally, seldom wholly pendent or erect. -- Leaves moderately pubescent. Leaf segments elongate, linear or slightly spatulate (on sterile shoots more distinctly spatulate), c. 0.4--0.6(--0.7) mm broad, acute--subacute. -- Synflorescence rather lax--moderately compact, with branches of a primary or, usually, secondary order. -- Capitula c. 4--5 mm long, often clustered in larger aggregates. -- Inner phyllaries c. (3.0--3.4--4.0 mm x 1.3--2.0 mm, sparsely pubescent. -- Florets c. 4--9(--11). Corolla with somewhat elongate-triangular lobes c. 0.40--0.60 mm x 0.30--0.50 mm. Corolla length/lobe length ratio c. 4.5--8.0. -- Achenes rather elongate, c. 1.6--2.6 mm x 0.8--1.2 mm, with ridges c. (50--75--100  $\mu$  broad.

ILLUSTRATIONS: Fig. 103.

FLOWERING PERIOD: End of August--September.

HABITAT: The substrate of the shores of the Baltic and its outlets is generally a more or less sandy mud. The tides are very much smaller than in western Europe, and the beaches are also usually higher. The vegetation is dominated by grasses and has to some extent been influenced by a long period of grazing.

The composition of the vegetation varies with the salinity of the sea. Along the outlets of the Baltic the salinity fluctuates

around 1 % (0.8--1.4 %), along the coast of Småland around 0.5--0.7 %. In Denmark, Germany and Skåne A. maritima is found in a belt along the shore (sometimes a short way up from the shoreline along ditches), often but not exclusively in marsh vegetation, viz., in the lower Festuca rubra--Agrostis stolonifera zone together with Juncus gerardi and Plantago maritima, and rarely, Limonium vulgare. A. maritima may occur also in grass vegetation dominated by Agropyron repens and Festuca rubra, or even on shores with an otherwise sparse plant cover. On the south-eastern coast of Sweden, where A. maritima ssp. maritima has previously been found extremely rarely, the tidal range is insignificant though seasonal and short-term variations can be considerable. In the central and upper geolittoral Juncus gerardi is the dominant species together with Festuca rubra and scattered Glaux maritima and Triglochin maritimum.

#### The North Sea Form Series

The distribution of A. maritima is more or less continuous on the Atlantic coasts of north-western Europe from western Jylland to the IJsselmeer in the Netherlands. Scattered localities of approximately the same salinity (c. 3 %) are also to be found on the north-eastern coasts of Jylland, and as the populations here are morphologically more or less intermediate between the North Sea populations and the populations on the Danish islands there is no distinct boundary between this and the Baltic Form Series. Between the populations in the north-western and south-western Netherlands there is a rather long gap owing to the marsh-less sandy coast between the Helder and the Hague, but morphologically the populations are distinctly connected with each other and also via the few Belgian populations with the French populations.

DESCRIPTION: Rhizome usually long and horizontal--slightly ascending, c. (2--3--6(--7) mm in diam., moderately lignified. -- Stems usually c. 20--40 cm, moderately(--strongly) suffrutescent, moderately--rather densely pubescent (grey--greyish-white), moderately branched. Branches c. (3--5--10(--15) cm, wholly or (usually) distally pendent, seldom erect. -- Leaves moderately--rather densely pubescent. Leaf segments linear (sometimes rather elongate) or



slightly spatulate (on sterile shoots more distinctly spatulate), c. 0.4--0.7 mm broad, acute--subacute. -- Synflorescence rather lax, with branches of a primary or secondary order. -- Capitula c. 3.5--5 mm long. -- Inner phyllaries c. (3.0--)3.2--4.0 mm x (1.0--)1.2--1.9(--2.0) mm, sparsely--moderately pubescent. -- Pistils c. 3--5. Corolla with somewhat elongate-triangular lobes c. 3.40--3.55 mm x 3.35--3.45 mm. Corolla length/lobe length ratio c. 5.5--9.0. -- Achenes elongate, c. 1.9--2.8 mm x 0.8--1.3 mm, with ridges c. 50--100  $\mu$  broad.

ILLUSTRATIONS: Fig. 104.

FLOWERING PERIOD: End of August--beginning of September.

HABITAT: The substrate of the marshes on the north-eastern coasts of Jylland is generally a muddy sand. The vegetation is dominated by grasses. A. maritima occurs in the central and upper geolittoral, usually in a belt along the shore in the drift-line, which is situated in the middle of a Festuca rubra--Agrostis stolonifera society. In this zone Juncus gerardi and Plantago maritima are often found as subdominants.

Some of the W. Danish and German marshes have rather sandy soils, but the majority of the North Sea marshes have firm clayey soils. Extensive areas, especially on the islands, are occupied by this type of marsh in which grasses are not so predominant as in the more sandy type. A. maritima covers large areas in the lower Festucetum rubrae, in which Limonium vulgare and Plantago maritima are important codominants. Juncus gerardi and Armeria maritima are also found in this association.

Tides are of great importance on this type of shore. At high tide A. maritima is sometimes covered by the sea (salinity c. 3 ‰). As the tide reaches far up, a halophytic vegetation also grows along the ditches a long way from the shore. Thus, A. maritima is found along ditches growing in long belts, often together with Limonium sp. On the mainland coast, where many marshes have been reclaimed, A. maritima is generally found colonizing drainage ditches and also to some extent growing along sea-walls.

## The French Form Series

In the province of Zeeland (the Netherlands) where there are many islands and the coastline thus is extensive, A. maritima is still fairly frequent, but from Belgium and southwards the species becomes increasingly rare occurring mostly in estuaries and around salines near the coast. The species has its southern-most locality near the Spanish border. Although the French plants are generally rather like the German and Dutch populations, they have evolved certain characteristics of their own, and they also have come in common with the British populations. Many of the French marshes are also rather similar in type to those on the British side of the Channel. Both in morphology and habitat the populations in northern-most France, Belgium and Zeeland are intermediate between populations typical of the North Sea and the French Form Series.

DESCRIPTION: Rhizome usually fairly long and horizontal--slightly ascending, c. (2--3--5(--7) mm in diam., moderately(--strongly) lignified. -- Stems usually c. (15--20--40(--50) cm, moderately--rather strongly suffrutescent, moderately--rather densely(--densely) pubescent (grey--whitish), moderately branched. Branches c. (1--3--10(--15) cm, usually wholly or distally pendent, not seldom erect. -- Leaves moderately--densely pubescent. Leaf segments often relatively short, (linear--spatulate, c. (0.5--0.6--0.9(--1.2) mm broad, subacute--almost blunt. -- Inflorescence rather lax--moderately compact, with branches of a primary or secondary order. -- Capitula c. 3.5--5(--6) mm long. -- Inner phyllaries c. (3.1--3.5--4.1(--4.5) mm x (1.2--1.4--2.0(--2.2) mm, rather sparsely--moderately pubescent. -- Florets c. 3--6(--8). Corolla with slightly elongate- or equilaterally triangular lobes c. (0.30--0.35--0.45(--0.50) mm x (0.25--0.30--0.45(--0.50) mm. Corolla length/lobe length ratio c. 5.5--8.0(--9.0). -- Achenes rather elongate, c. 1.8--2.5 mm x 0.9--1.2(--1.3) mm, with ridges c. 50--100  $\mu$  broad.

Certain differences can be discerned between the French populations north and south of the Breton peninsula, though these mostly consist of slightly differing frequencies within a similar range of variation. Thus, the northern populations include a proportionately greater number of plants with tall stems, large capitula and phyllaries, and a dense pubescence.

ILLUSTRATIONS: Fig. 105.



FLOWERING PERIOD: September--beginning of October.

HABITAT: In Belgium and France extensive marsh areas are rather rare and have become increasingly rarer, as much of the wild marshland has been and still is being reclaimed. Only in estuaries are more extensive marshes still to be found, e.g. in the Somme estuary, and then the major part of the marsh is often dominated by an Artemisietum maritimae, generally with Limonium vulgare and Plantago maritima as subdominants. In most estuaries, however, the marsh vegetation is restricted to banks along the arms of rivers and creeks, with Artemisia maritima in a band above a Halimione portulacoides zone. Limonium vulgare frequently occurs as an associated species, and also Agropyron repens, Festuca rubra, Plantago maritima and, though more seldom, Agrostis stolonifera. In France south of the Breton peninsula A. maritima and other marsh vegetation is commonest in salines near the coast, along canals and creeks, and with an increasing proportion of mud in the substrate Halimione becomes more frequent and often occurs in large numbers in the Artemisietum and, predominantly, in a fringe below this zone. Another associated species characteristic of these southern marshes is Inula crithmoides, but Agropyron repens, Festuca rubra and Limonium vulgare are still rather frequent.

### The British Form Series

In Great Britain A. maritima is rather rare except in southeastern England. According to herbarium sheets from the preceding century, the species was more frequent then but the area of distribution has since become reduced, probably following the disappearance of considerable areas of wild marshland through reclamation. From Ireland only three localities are known to the author.

The populations of A. maritima in Great Britain have morphologically much in common with both the North Sea and French Form Series (in the latter case the frequently large heads and broad, short leaf segments, for example). In some respects, however, they resemble populations on the shores of the Baltic and its outlets, e.g. in degree of branching and pubescence (frequently richly branched and rather sparsely pubescent).

DESCRIPTION: Rhizome usually fairly long and horizontal--slightly ascending, c. (2--3--6(--7) mm in diam., moderately--strongly lignified. -- Stems usually c. (20--25--40(--50) cm, moderately--rather strongly suffrutescent, moderately(--rather densely) pubescent (greyish-green--grey), moderately--richly branched. Branches c. 3--15(--20) cm, usually pendent distally, seldom wholly pendent or erect. -- Leaves moderately(--rather densely) pubescent. Leaf segments often relatively short, linear--somewhat spatulate (on sterile shoots more distinctly spatulate), c. 0.5--0.8(--1.2) mm broad, acute--subacute(--almost blunt). -- Synflorescence rather lax--moderately compact, with branches of a primary or secondary order. -- Capitula c. 3.5--5(--6) mm long. -- Inner phyllaries c. 3.2--4.0(--4.2) mm x (1.2--1.4--1.8(--2.0) mm, sparsely--moderately pubescent. -- Florets c. 3--7. Corolla with equilaterally--somewhat elongate-triangular lobes c. (0.35--0.40--0.50(--0.55) mm x 0.30--0.45 mm. Corolla length/lobe length ratio c. 5.5--8.0(--9.0). -- Achenes rather elongate, c. 1.8--2.4 mm x 0.8--1.2 mm, with ridges c. 50--75(--100)  $\mu$  broad.

Large, richly branched specimens with long leaves are more frequently found in south-eastern England than elsewhere in Britain. It seems that large phyllaries are also more frequent in this area than anywhere else, but a distinct pattern of variation is difficult to discern as large-headed plants are common also in W. English and in Irish populations.

ILLUSTRATIONS: Fig. 106.

FLOWERING PERIOD: September.

HABITAT: The marshes on the west coast of Great Britain have much in common with the Scandinavian marshes. Thus they are characterized by a high proportion of sand in the soil, and grasses are predominant in the vegetation. However, the difference between high tide and low tide is here considerable as in other parts of Great Britain in contrast to Scandinavian conditions. Most of the A. maritima localities on the west coast are concentrated to the Severn estuary in Gloucestershire and Somerset. The species grows in the lower part of a Festuca rubra--Agrostis stolonifera zone, often together with Plantago maritima, Glaux maritima and Armeria maritima.

The marshes of southern England are more like the marshes on the other side of the Channel, i.e. rather muddy and with a characteristic Halimionetum. Artemisia maritima frequently occurs together with



Festuca rubra, Puccinellia maritima, Halimione portulacoides, Plantago maritima, Glaux maritima and Limonium vulgare. The marshes in south-eastern England (e.g. Canvey Island, Mersea Island) are also of a similar type, with A. maritima often growing in a zone along the sea-walls, above the Halimione portulacoides zone but with scattered individuals of this species intermixed with other species more characteristic of the Artemisietum. Further northwards the marshes grow increasingly like those on the North Sea coast of the mainland. The soil contains high proportions of clay and silt. Within the often extensive marshlands A. maritima is abundant in the lower part of the Festucetum (above the Puccinellietum), together with Festuca rubra, Plantago maritima, Armeria maritima and Limonium vulgare, and in places with scattered individuals of Juncus gerardi, Plantago coronopus, Cochlearia officinalis and Aster tripolium. According to Chapman (1960) many of the British North Sea marshes will in time become more like the typical Channel marshes, as a consequence of the planting (or spontaneous spreading) of Spartina townsendii, which already plays a great part in the succession of marsh communities on both sides of the Channel.

### The Inland Form Series

In Thüringen (central Germany) there is a small area of salt-marshes that owe their origin to the solution of subterranean salt deposits. Compared with former times very small areas are now occupied by a halophytic flora, including A. maritima. The species has here its only inland localities, the main occurrence nowadays being in Solgraben, near the town of Artern.

DESCRIPTION: Rhizome rather long and horizontal--slightly ascending, c. 4--7 mm in diam., moderately lignified. -- Stems c. (20--) 30--60 cm, moderately--strongly suffrutescent, sparsely--moderately pubescent (dull green--greyish-green), soon glabrous at the base, moderately branched. Branches c. 5--15(--20) cm, erect or distally pendent, seldom wholly pendent. -- Leaves sparsely--moderately pubescent. Basal leaves soon dropping off. Leaf segments relatively short--rather elongate, linear or slightly spatulate (on sterile

shoots more distinctly spatulate), c. 0.5--0.7 mm broad, acute--subacute. -- Synflorescence rather lax--moderately compact, with branches of a primary or secondary order. -- Capitula c. (3.5--) 4--5 mm. -- Inner phyllaries c. (3.0--) 3.2--4.0 mm x (1.0--) 1.3--2.0(--2.2) mm, sparsely--moderately pubescent. -- Florets c. 3--7(--11). Corolla with equilaterally--slightly elongate-triangular lobes c. 0.40--0.55 mm x 0.35--0.50 mm. Corolla length/lobe length ratio c. 5.0--7.5. -- Achenes fairly elongate, c. 1.9--2.4 mm x 0.8--1.2 mm, with ridges c. 50--75(--100)  $\mu$  broad.

ILLUSTRATIONS: Fig. 107.

FLOWERING PERIOD: September--beginning of October.

HABITAT: The halophytic vegetation of Solgraben is found in a small depression, where the ground is periodically flooded by water from a salt spring with a concentration of mineral salts as high as 3.2--4.2 %. The annual rainfall is low (in Artern 444 mm per year).

A. maritima is found on elevated areas along the edges of a rather moist Juncus gerardi--Glaux maritima salt meadow.

### Localities

NORWAY. Hvaler. Asmalö (S).

SWEDEN. Bohuslän. Askim: Billdal, north of the station (LD); Killingsholmen (LD, S). -- Kville: Hällan, northern side of the Jorefjord (UPS). -- Lycke: Karholmen N, Juteskäret (LD, S). -- Lyse: Trälebergskile, inner part of the bay (LD, S). -- Malmö: Bredviken (S). -- Marstrand: Small island near Koön (LD, S); Marstrandsön, Skallen c. 300 m S (LD). -- Morlanda: Käringsön (S). -- Öckerö: Burön (LD); Hyppeln (LD, UPS); Hälsö (S); Hönön, Röd c. 1500 m W (LD); Öckerön, near the northern point (LD); Öckerön, Norgården c. 400 m WSW (I. Kärnefelt); Rammen, the south bay (I. Kärnefelt); Rörön, Apelvik (LD); Rörön, south-east point (I. Kärnefelt). -- Rönnäng: Kårevik (S). -- Skaftö: Gåsö (Sunesson 1968); Koskär (op. cit.); Långholmen (op. cit.); Skutevik SE (op. cit.); Storön, west shore (op. cit.); Sörhålet N (LD); Tjällsö, south shore



(Suneson 1968). -- Stenkyrka: Stockevik SW (S). -- Styrsö: Krokholmen (LD, S, UPS); Styrsön, southern point (LD, S, UPS); Styrsön, the church c. 1650 m S and 250 m W (LD); Tistlarne (LD, S, UPS, WU); Small island west of Vallholmen (S); Vinga (LD, S, UPS); Vrångö (S). -- Tjärnö: Nordkoster, Valnäsbukten (LD, S). -- Halland. Landa: Frillesås c. 2000 m N, Lannabukten (LD); Rågelund (LD, S). -- Morup: Glommen (LD, S); Morups tånge (LD). -- Ölmevalla: Åsa (LD). -- Onsala: Malön (S); Råö (S); Near Råö, Fjärhals SSW (S). -- Tvååker: Galtabäck (LD). -- Varberg: Along the road to Getterön (LD, UPS). -- Värö: Bua (LD, UPS). -- Skåne. Barsebäck: Barsebäckshamn (LD, UPS); Saltvik (LD). -- Brunnby: Lerhamn (LD). -- Bunkeflo: Sigfridsborg (LD); Stenören (LD); Strandhem (LD). -- Burlöv: Arlöv (E, LD, S, UPS, WU). -- Eskilstorp: Eskilsdal c. 1500 m WSW (LD); Kuddarna (LD). -- Falsterbo: Flommen (LD). -- Gässie: Grönahill c. 1200 m W (LD); Near the border between the Gässie and Hököpinge parishes (LD). -- Hallands Väderö: Sandhamn N (Vallin 1936). -- Hälsingborg: South of the harbour (LD). -- Hököpinge: Janstorp (LD, S, UPS). -- Jonstorp (LY). -- Landskrona: Landskrona (FI, JE, LD, S, UPS, W); Östra Fäladen (S). -- Löddeköpinge: Vikhög c. 1500 m N, Saltviken (LD). -- Lomma: Lomma (E, FI, JE, LD, LY, M, S, UPS, W, WU). -- Malmö: Malmö (LD, S, UPS); Frihamnen (LD); Industrihamnen (LD); Limhamn (JE, LD, LY, M, S, UPS, WU); Ribersborg (LD); Sibbarp (LD); Between Sibbarp and Stenören (LD). -- Östra Vemmenhög: Dybäck, Bingsgården (LD). -- Saxtorp: The mouth of the river Saxån c. 1300 m SSE (LD). -- Skanör: North of the church (LD); West of the church (LD, UPS); Ljunghusen (LD). -- Stora Hammar: Stora Hammar (LD, UPS); Kungstorp (LD); Lilla Hammar c. 2000 m NNW (LD, UPS). -- Tofta: Häljarp (LD, M). -- Torekov: Torekov c. 700 m S (LD). -- Tygelsjö: Sjötorp c. 1000 m NW (LD). -- Västra Klagstorp: Klagshamn (LD). -- Vellinge: Vellinge (JE, LD, M, S, UPS, WU); Olsborg c. 500 m W (LD). -- Ven: Northern coast, near the brick factory (LD). -- Blekinge. Torhamn: Torhamn (LD, S, UPS); Böljaskär (UPS); Tvegölja (LD). -- Småland. Åby: Björnö, Rönnholmen (S, UPS). -- Västervik: Gränsö (S).

DENMARK. Maribo. Askö (C). -- Falster, Nyköbing (C). -- Lolland: Guldborg N (C); Høvaenge Skov (C); Hyllekrog (C); Rødby (C). -- Suderø, outside north-western Falster (C). -- Rågård (C). -- København. Amager: Dragør (C, LD, UPS); Faelled (C); Kalveboderne (C); Kastrup (C); Kongelunden S (C, LD, S); Tårnby (C). -- Avedøre strand (C, LD). -- Flaskekroen (C, E, G, JE, LD, M, S, UPS,

W). -- Gundsömagle c. 2000 m WSW, Vigen (LD). -- Jersiestrand (C). -- Köbenhavn (C, FI, M). -- Ölbylyng (C). -- Saltholm: South shore (C); Holmegaard c. 300 m NE (LD, S, UPS). -- Vallensbaekstrand (LD). -- Veddelev, north of the village (LD). -- Vesterfaelled (C, LD, S, UPS). -- Frederiksborg. Frederikssund (C, UPS). -- Frederiksværk (C, LD, UPS). -- Graese c. 2000 m W (LD). -- Hanehoved (C). -- Jaegerspris (C). -- Lille Kregme (LD). -- Kulhuse (C). -- Holbaek. Eriksholm (C). -- Gudmindrup (M). -- Hönsinge Lyng (C). -- Kalundborg (S). -- Nekselö (M). -- Reersö (C). -- Samsö: Besser rev NE, Lindholm (C); Lushage (C). -- Vester Lyng, on the Sejerö Bay (C). -- Sorö. Agersö, Draget (C). -- Enö (C). -- Glaenö (C). -- Odense. Agersnaes (LD). -- Brandsö, south coast (C). -- Gamborg (C). -- Hofmannsgave (C). -- Middelfart W (C). -- Stige, along the canal (LD, UPS). -- Toröhuse (C). -- Svendborg. AErö: AErösköbing (C); Gråsten Nor (C); Halmö (C); Marstal Havn, Kalkovnsöen (C); Ommels Hoved (C); Nyland (C). -- Avernakö, Hovedsö (C). -- Birkholm (C). -- Langeland: Bagenkop (C); Keldsnor (C). -- Nyborg, Slipshavn (C). -- Siö: Siö (UPS); Lille Fugleö (C). -- Strynö, Vester Mölle S (C). -- Strynö Kalv (C). -- Tåsinge, Vårö (C). -- Haderslev. Årö, Årö Kalv (C). -- Halk c. 3500 m NE, Flovt Strand (LD). -- Vejle. Hejlsminde (C, LD). -- Hjarnö (C). -- Kolding (C). -- Skanderborg. Stensballe (C). -- Vårsö (C). -- Århus. Endelave, western point (C). -- Randers. Bönnerupstrand (C). -- Knebel Vig (C). -- Lystrupstrand (C). -- Södring c. 1500 m SSW, Vasehuse (LD). -- Udbyhöj, south side of the Randers fjord (C, S, W). -- Ålborg. Als (W). -- Als Odde (C). -- Egense c. 3000 m S, Klattrup (LD). -- Hou (C). -- Öster Hurup (C). -- Sebbersund (C). -- Skiber Huse (C). -- Hjörning. Frederikshavn: Frederikshavn N (C); Rönnerne (C). -- Hirsholm (C). -- Jerup c. 1000 m ENE (LD). -- Laesö: Langerön (C); Österby (C); Nordre Rönner (C). -- Lyngså c. 2500 m SE (LD). -- Ribe. Allerup (C). -- Fanö: Fanö (C); Sönderho (S, UPS). -- Hjerting SE (C). -- Ho (LD). -- Langli (C). -- Mandö (LD). -- Ribe (C). -- Store Darum c. 1500 m W (LD). -- Tjaereborg c. 2000 m SW (LD). -- Vester Vedsted (C). -- Tönder. Emmerlev, the Höjer canal c. 1000 m N (LD). -- Hviding c. 2000 m NW (LD). -- Römö: C. 200 m north of the road to the mainland (LD); Havneby (C, M). -- Römödaemningen, c. 3000 m from the mainland (LD).

GERMANY. Sachsen-Anhalt. Artern, Solgraben (E, FI, G, HAL, JE, K, L, LD, LY, M, S, UPS, W, WU). -- Between Artern and Kachstedt (JE). -- Aschersleben, Harkerode, Burg Arnstein (cult., FI, JE, L, M, WU). -- Eisleben: On saline lake (E, HAL, JE, UPS, W); Oberröbblingen (W); Rollsdorf, on Mansfelder See (G, HAL, JE, LD, W); Seeburg (S, W). --



Kachstedt (JE). -- Kelbra, Numburg, saline spring (cult? JE). -- Near Schönebeck (S). -- Mecklenburg. Barth, Vogelsang (G, JE, L, M, WU). -- Hiddensee, Neuendorf (JE). -- Rügen: Rügen (E, JE); Altefähr (JE). -- Stralsund: Bock (JE); Between Risdorf and Wendisch Langendorf (WU). -- Usedom, Heringsdorf (JE). -- Wismar: Wismar (E, S); Poel (JE, K, LD, W, WU); Poel, Brandenhusen SE (JE); St. Jakob (M). -- Wustrow peninsula (JE, L, LY, S, W, WU). -- Schleswig-Holstein. Angeln: Kappeln c. 2000 m NNE, near Rabel (LD); Maasholm (FI, JE). -- Dithmarschen: Meldorf (FI, JE); Wesselburenerkoog c. 3000 m NW (LD). -- Eiderstedt: St. Peter S (M); Borsthusen (LD). -- Fehmarn: Fehmarn (E); Between Burgstaaken and Wulfer (JE). -- Helgoland (JE). -- Near Lübeck (FI). -- Nordfriesische Inseln: Amrum, Wittdün (LD); Föhr (JE, M); Föhr, Oldsum c. 2000 m NNE (LD); Nordstrand, Elisabeth-Sophien-Koog (LD); Nordstrand, Süderhafen (LD); Nordstrandischmoor, Neuwarft SE (LD, M); Pellworm, Ostersiel (LD); Sylt, near Kampen (JE, W); Sylt, Keitumer Bucht (WU); Sylt, List (JE, LD, S, UPS); Sylt, Morsum (LD, M, W); Sylt, Wenningstedt (JE); Sylt, Westerland (JE, M). -- Nordfriesland: Husum (JE, W); Husum c. 1500 m W, Dockkoog (JE, K, LY); Husum SW, Finkenhäuser Hallig (JE); Husum, Padelacker Hallig (JE); Husum c. 5000 m NW, Schobüll (LD); Klanxbüll c. 5000 m SW, Friedrich-Wilhelm-Lübkekoog (LD); Ockholm c. 2000 m W (LD). -- Nordholstein: Fehmarnsundbrücke c. 1000 m S (LD); Heiligenhafen c. 1000 m ENE (LD); Hohwacht (JE). -- Probstei, Stein (L). -- Niedersachsen. Butjadingen, Langwarden c. 1500 m NW (LD). -- Land Hadeln, Cuxhafen (HAL, JE, L, LY, S, W). -- Ostfriesische Inseln: Borkum (JE, L, M, W); Juist, below and west of the village (LD); Langeoog, c. 200 m east of the village (LD, M, S); Norderney (E, JE, U, WU); Wangerooge (LD, M). -- Ostfriesland: Emden (M); Kniephausersiel (M); Minnen c. 2000 m NW (LD); Norden (JE); Rüstersiel (M); Varel (E, W, WU); Voslapp c. 1500 m N (LD); Westeraccumersiel c. 2000 m NW (LD); Westermarsch c. 2000 m WSW (LD); Wilhelmshaven (M, U).

THE NETHERLANDS. Groningen. Hornhuizen c. 4000 m WNW (LD). -- Oosteinde c. 4000 m NE, Oudeschip (LD). -- Friesland. Ameland, Nes, below the village (LD). -- Griend (FI, G). -- Harlingen (U, WU). -- Minnertsga c. 4000 m NW, Firdgum c. 3000 m NNW (LD). -- Schiermonnikoog (L). -- Staveren (U). -- Terschelling: Midslan S (G); Boschplaat (U); Oosterend (U); Westterschelling (L). -- Vlieland, Oost-Vlieland (L, U). -- Wierum (LD). -- Overijssel. Noordoostpolder: Oostdijk, between Ens and Emmeland (U); Urk (U). -- Noord Holland. Den Helder (L, U, W). -- Huisduinen (U). -- Marken, eastern side

(L). -- Texel: De Cocksdorp (L, LD); Sluftervlahte (L). -- Wieringen, Woudstrand (L). -- Zuid Holland. Voorne: Hellevoetsluis W (G, K); Oostvoorne (U). -- Zeeland. Noord-Beveland (U). -- Saeftingen, the mouth of the Schelde R. (BR). -- St. Philipsland (BR). -- Schouwen, Kondekerke (U). -- Tholen (LY). -- Vlissingen (BR, U). -- Walcheren, near Middelburg along the canal (BR). -- Zeeuws-Vlaanderen: Terneuzen (BR, FI, G, HAL, LD, LY); Between Terneuzen and Philippine (BR). -- Zuid-Beveland (U). -- Noord Brabant. Bergen op Zoom (U).

BELGIUM. Antwerpen. Lillo, the mouth of the Schelde R. (BR). -- Zandvliet, the mouth of the Schelde R. (BR). -- Oost Vlanderen. Kieldrecht, near the mouth of the Schelde R. (BR). -- West Vlanderen. Heist (BR). -- Knokke, Zwiijn (BR, JE, S). -- Lombardsijde (BR). -- Nieuwpoort, the mouth of the Yser R. (BR, FI, G, L, S). -- Oostende (BR).

FRANCE. Nord. Dunkerque (BR). -- St. Pol-sur-Mer (FI). -- Pas de Calais. Boulogne-sur-Mer (E, G, K). -- Somme. Abbéville: Cambron (BR, FI, G, JE, K, P, W); Laviers (BR, FI, W). -- Cayeux-sur-Mer (G). -- Le Crotoy (FI, G). -- Mouth of the Somme R. (E, G). -- Noyelles-sur-Mer (FI). -- St. Valéry-sur-Somme c. 4000 m NW, Le Hourdel (BR, JE, LD). -- St. Valéry-sur-Somme c. 800 m WNW, Mollières (BR, FI, G, LD, P). -- Seine-Inférieure. Dieppe (G). -- Le Havre (LY). -- Le Tréport (BR, G). -- Calvados. Cabourg, the mouth of the Dives R. (BR, LD). -- Caen, the mouth of the Orne R. (W). -- Pont de Ranville, the mouth of the Orne R. (P). -- Trouville, the border of the Touques R. (G, S). -- Manche. Cherbourg (W). -- Lessay (BR). -- Quinéville (G). -- Réville (G). -- St. Germain-sur-Ay (M). -- Côtes du Nord. Lancieux (K). -- Finistère. Ile d'Ouessant (FI). -- Morbihan. Vannes, Sène (LD, UPS). -- Loire-Atlantique. Le Pouliguen (K). -- Vendée. Beauvoir-sur-Mer c. 2000 m NW, Epoids (LD). -- Ile de Noirmoutier (FI, M). -- L'Ile d'Olonne c. 2400 m NNW, La Salaise (LD). -- Les Sables d'Olonne (BR, FI, LD, P, UPS, W). -- Les Sables d'Olonne c. 3000 m NNW, La Girvière (LD). -- St. Gilles: St. Gilles (UPS); La Roche-sur-Yon (W). -- St. Martin-de-Brem c. 800 m S, La Gachère (W). -- Charente-Maritime. Aytré, Pointe de Roux (FI). -- Chaillevette (G). -- Châtelailillon c. 4000 m SSE, Le Marouillet (FI, G). -- Ile de Ré (FI, JE). -- Near Marennes (P). -- Near La Rochelle (FI, G, JE, LD, M, P, S, W). -- La Rochelle SSE, Angoulins (LD, S). -- La Rochelle c. 4000 m N, Pointe de Plomb (FI, LD). -- Saujon c. 4000 m WNW, Fontbedeau (P). -- Gironde. Between Pointe de Grave and le Verdon-sur-Mer (G, LD). -- Le Verdon-sur-Mer (G, LY). -- Basses Pyrénées. Bayonne (G). -- Biarritz (FI).



GREAT BRITAIN. England. Cheshire: Bromborough (LY). -- Devon: Barnstaple, banks of the R. Taw (UPS). -- Essex: Canvey Island (BR, K, LD, S); Clacton-on-Sea (K); Mersea Island, near the bridge to the mainland (LD); Between Southend-on-Sea and Leigh-on-Sea (LD). -- Gloucestershire: Near Avonmouth (LD, S); Mouth of the R. Avon, near Bristol (W). -- Isle of Wight: On the west side of the creek at Newport (JE, LD, LY). -- Kent: Northfleet Hope (K); Pegwell Bay (BR, LY); Sandwich (BR). -- Lincoln: Skegness (K). -- Norfolk: Blakeney (BR, S); Cley c. 2000 m E, Salthouse (LD); Hunstanton (K); Hunstanton c. 2000 m NE, Thornham (LD); Near South Heacham (K); Wells (FI, LD, S, W). -- Somerset: Burnham-on-Sea (LD, M, W); Portbury Flats (K); Uphill (G, LD). -- Suffolk: Between Aldeburgh and Thorpeness (FI); Southwold (K). -- Sussex: Littlehampton (W); Shoreham-by-Sea (L). -- York: North Riding, Middlesbrough (BR, G). -- Wales. Glamorgan: East Aberthaw (K). -- Merioneth: Barmouth (K). -- Pembroke: Between St. David's and Invercithen (G). -- Scotland. Angus: Forfarshire (LY, M). -- East Lothian: Tynninghame estuary (FI, UPS). -- Renfrew: West of Glasgow (K). -- Wigtown: Mull of Galloway (G, S). -- Northern Ireland. Down: Between Killough and St. John's Point (K).

EIRE. Dublin (FI). -- Galway Bay, Oranmore (M).

Artemisia maritima L. ssp. humifusa (Fries ex Hartman) K. Persson stat. nov.

A. maritima L. var. humifusa Fries ex Hartman 1879 p. 8. -- A. maritima L.  $\beta$ . humifusa Fries 1845 p. 2 (excl. syn. Willd.), nomen nudum. -- Original collection: Gotland, Boxarfve. Leg. P. C. Afzelius (UPS, Herb. Hartm., lectotype).

ILLUSTRATIONS: Figs. 108--109 (habit), 101 B (distribution).

Rhizome mostly rather short, ascending, c. 2--3(--5) mm in diam., moderately lignified. -- Stems decumbent--ascending, c. 5--25(--40) cm, slightly(--moderately) suffrutescent, densely pubescent (greyish-white--white), unbranched--moderately branched. Branches c. 0--3

(--7) cm, as often erect as distally or wholly pendent. -- Often a very rich production of small sterile shoots. -- Leaves densely pubescent. Laminae of lower cauline leaves c. 5--18 mm x 4--13 mm, with short, linear--spatulate, usually blunt segments c. 0.4--0.7 (0.8) mm broad. -- Synflorescence usually simple in structure, often spicate, moderately compact, often wholly secund, with sessile --almost sessile capitula on panicle branches of primary (seldom secondary) order (or spicately arranged). -- Capitula c. 3--4(5) mm long, usually erect. -- Inner phyllaries narrowly elliptic(--obovate), c. 3.0--3.6 mm x 1.0--1.7 mm, moderately pubescent, scarious margins c. 0.3--0.6 mm broad. -- Florets c. 3--7. Corolla c. 2.4--2.8(3.0) mm long, corolla lobes rather broadly triangular, c. 0.35--0.45(0.50) mm x 0.35--0.45(0.50) mm. Corolla length/lobe length ratio c. 5.0--7.0(8.0). Anthers c. 0.8--1.2(1.4) mm long, apical appendage c. 0.25--0.35 mm long. Style branches c. (0.4--0.5--0.7) mm long. -- Achenes c. 1.5--2.0(2.3) mm x 0.7--1.0 mm, with ridges c. 50--75(100)  $\mu$  broad.

DISTRIBUTION: Marshes, stony shores and wide flat sea-shore meadows on limestone on coasts of Öland, Gotland and Saaremaa (Ösel).

FLOWERING PERIOD: August(--beginning of September).

HABITAT: The brackish marshes of Öland, Gotland and Saaremaa form a somewhat specialized habitat on account of the calcareous substrate and the arid climate. The substrate is mostly a moraine, but it often consists of a thin layer of soil on limestone rock. The latter type is characteristic of the wide, flat salt-marsh that is the most typical biotope of ssp. humifusa, above all on Öland. The subspecies here often occurs in large populations covering considerable areas, sometimes in association with Agrostis stolonifera and Juncus gerardi, sometimes on otherwise bare soil. On shores with richer vegetation Agrostis stolonifera, Festuca rubra, Juncus gerardi, Triglochin maritimum, Plantago maritima and Armeria maritima are found in the Artemisietum. Most of these shores are influenced by grazing cattle.

On Öland (Persnäs, Föra) ssp. humifusa is also rarely found in a kind of "alvar" vegetation on wide, flat shores, usually in a Mollia tortuosa--Agrostis stolonifera association, but sometimes even in the arid Cornicularia aculeata--Festuca ovina association.

On Gotland the beaches are often higher, and ssp. humifusa then surrounds the edges of shallow depressions, above a Puccinellietum maritimae.

The author has not personally been able to study the localities



of ssp. humifusa on Saaremaa, but according to Lelley (1958) the subspecies here usually grows in an Agrostis stolonifera--Juncus gerardi association, together with Plantago maritima, Triglochin maritimum, Centaureum vulgare and Leontodon autumnalis.

Apart from growing on these more or less marsh-like shores ssp. humifusa also occurs on rather high, stony beaches with very sparse vegetation. Such shores are especially frequent on Gotland. The subspecies often occurs in the upper and central geolittoral as the only plant species (excepting some lichens), growing in long belts in the drift-line, fertilized by seaweed. Ssp. humifusa has here often taller, more lignified stems, is more richly branched with longer branches and has longer leaves with broader segments than the typical humifusa forms (Fig. 109).

### Localities

SWEDEN. Öland. Alböke: Karse c. 900 m NE, Stora fjärden (LD); Kåreholm (LD, UPS). -- Böda: Lilla Grundet, Grankullaviken (LD). -- Bredsätra: Kapelludden, near the lighthouse and the chapel (LD, S, UPS); Långöre (LD); Nedre Sandby c. 1200 m ESE (LD). -- Föra: Husballa (LD, UPS); On the bay Södviken (LD, UPS). -- Källa: Källahamn (LD, S, UPS, W). -- Löt: Karse c. 500 m ESE (B. Nilsson). -- Persnäs: Persnäs (E, S, UPS); Hallnäs (LD, UPS, WU); Trosnäs SE, Södra holmen (UPS); Östra Södvik, north-eastern corner of the bay Södviken (LD, S). -- Runsten: Runstensstrand (UPS). -- Gotland. Angä: Skarnvik (LD). -- Boge: Boge vik, northern shore (S); Boge vik, southern shore near the mouth (LD, UPS); Friggars (LD, WU); Tjölderviken (UPS). -- Burs: Herte c. 300 m WNW (LD); Hummelbosholm (LD). -- Eke: Eke strand (UPS). -- Fide: Fide, eastern shore (LD, S); Fidenäs (LD). -- Gammelgarn: Engmansviken (S). -- Gothem: Botvaldevik, Tummungs c. 500 m NW (LD, S, UPS); Nors (UPS); Sildungen (S, UPS). -- Grötlingbo: Grötlingboudd, inner part of the bay Gansviken (LD, S, UPS, W). -- Hablingbo: Petesvik (LD, S). -- Klinte: Klintehamn, Varvsholmen (E, LD, S, UPS, W, WU); Skansholme (UPS). -- Lärbro: Stora Hammars, on the bay Vägumeviken (LD,

S, UPS). -- När: Närs strand (S). -- Näs: Näsudden (LD). -- Öja: Boxarve (UPS); Burgsvik (LD, S, UPS, W); Stockvike (UPS). -- Rone: Ronehamn (LD, M, S, UPS). -- Sanda: Klintehamn c. 1000 m NNW (LD, UPS); Vivesholm (LD, S, UPS, W). -- Silte: Kvarnåkershamn (LD). -- Slite: Slite (LD, M, S, UPS, WU). -- Visby: Visby (LD, S, UPS); Kneippbyn (LD).

USSR, ESTONSKAYA SSR. Saarema. Eriksaare peninsula: south-west coast (TU); western coast (TU). -- Harilaid peninsula (TU). -- Kihelkonna (LE). -- Kuusnõmme peninsula: eastern coast (TU); western coast (LE, TU). -- Papissaare peninsula, the southern coast (TU). -- Pussa (TU). -- Tagamõisa (LY, W). -- Väike-Vilsandi, southern part (TU). -- Vilsandi, Vaika saared (TU).

#### ARTEMISIA VALLESIACA All.

Allioni 1774 p. 68. -- A. maritima L. ssp. vallesiaca (All.) Gams in Hegi 1928 p. 661. -- Original collection: without locality (TO, Herb. All., lectotype).

A. filaginoidea Weber in Stechmann 1775 p. 30 (excl. pl. Hisp.). -- The type material has been applied for unsuccessfully in most of the European Herbaria and has apparently been lost, but the description confirms the synonymy.

A. vallesiana Lamarck 1783 p. 269. -- The type material does not seem to be included either in Herb. Lam. or in other herbaria seen by the present author. The name vallesiana is perhaps only a misprint for vallesiaca, but Lamarck does not cite Allioni.

A. maritima L. κ. lercheana (Stechm.) Besser a. europaea Besser 1834 p. 37. -- Original collection: Switzerland, "Vallesia" (H, no. 1013640, lectotype).

Note: There has been some disagreement as to the actual year of publication in journal of Allioni's "Auctuarium ad Synopsis Methodicam Stirpium Horti Regi Taurinensis" (Mélanges de Phil. et Math. de la Société Royale de Turin V). Most authors agree on 1774 as the probable date of publication (Chiovenda 1912, Fuchs 1960, Stafleu 1967).



ILLUSTRATIONS: Figs. 111 (habit), 110 (distribution).

A suffrutex with a vigorously developed, strongly lignified, much-branched, usually ascending rhizome, c. 5--10(--15) mm in diam., with a rough and fibrous surface. Internodes c. 2--7(--10) mm long. A rich production of small rosette-bearing sterile shoots. -- Stems ascending, c. (10--20--40(--50) cm long, moderately--strongly suffrutescent, densely and persistently pubescent (greyish-white--white), weakly--moderately branched, usually above the middle, seldom from the base. Branches rather short, c. 0.5--6(--20) cm (longest in richly branching plants), erect (extremely seldom pendent distally). -- Lower cauline leaves petioled though often indistinctly, nearly always with large pinnatisect auricles, densely pubescent; persistent during the whole growth season. Laminae c. 7--15(--20) mm x 5--10 mm, 3--4-pinnatisect, with often crowded segments c. 0.3--0.5 mm broad, mostly linear with an acute or subacute apex, seldom blunt. Leaves on sterile shoots similar but more distinctly petioled, with blunter segments. Upper cauline leaves gradually smaller, uppermost very small, pinnatifid(--pinnatisect), seldom entire. Stomatal cells c. 22--34  $\mu$  long. -- Hairs on stems, branches and leaves T-shaped with very long arms, two or three basal cells. Glands c. 40--50  $\mu$  at broadest part (top), each gland consisting of eight secreting cells in two rows and two basal cells; present on all aerial parts (except achenes). -- Synflorescence rather compact (except in long-branched individuals), often congested and spicate, seldom secund; clusters of sessile or almost sessile, very seldom distinctly stalked, capitula on panicle branches of primary(--secondary) order. -- Capitula erect, oblong--elliptic(--ovate), c. 3--4(--5) mm long, with peduncles c. 0--0.5(--2) mm long. -- Phyllaries slightly spreading, more or less distinctly imbricate, acute or subacute, glandular; outer small, either narrowly elliptic, wholly herbaceous, or broadly triangular, mucronate with basally broad scarious margins; densely pubescent; inner elliptic--obovate, c. 3.0--4.2 mm x 0.9--1.4(1.6) mm, with scarious margins c. 0.7--0.4(--0.3) mm broad abruptly narrowing towards the base, herbaceous midrib region sometimes with red margins, linear--slightly spatulate with a subacute(--blunt) apex, moderately--densely pubescent on upper half; upper part of scarious margins sometimes ciliate with very coarse hairs. -- Florets c. 3--5(--7), all hermaphrodite. Corolla c. 2.5--3.0(--3.2) mm long, yellow or

slightly reddish, glandular, tubular, widening slightly in the upper part; corolla lobes 5, narrowly triangular, c. (0.35--0.45--0.60 (0.65) mm long. Corolla length/lobe length ratio c. 4.5--6.5 (7.0). Anthers c. (0.9--1.0--1.4 mm long, narrow, acutely appendaged basally; apical appendage narrowly lanceolate, c. (0.25--0.30--0.35 (0.40) mm long, acute. Pollen grains tricolporate, c. 16--23  $\mu$  in diam. (usually 18--20  $\mu$ ). Style longer or shorter than corolla, style branches flattened, c. 0.7--0.9 (1.0) mm long. -- Achenes broadly obovate, c. 1.6--2.1 mm x 0.9--1.2 mm, with low longitudinal ridges c. 75--150  $\mu$  broad. Style scar usually oblique, seldom surrounded by an inconspicuous bulge. -- Chromosome number  $2n=36$ .

The species is fairly uniform throughout the limited area of distribution. Only minor differences exist between the Swiss and Italian populations.

DISTRIBUTION: On dry calcareous mountain slopes (alt. c. 800--1000 m), usually southern or south-western slopes, in Switzerland (Valais) and Italy (Piemonte). According to Hegg, Landolt & Hitzel (1972) A. vallesiaca occurs also in Savoy (Montanvert), but no material from this locality has been seen by the present author.

The species has been reported from Krk and Rab (in the Gulf of Kvarner, Yugoslavia). The reports are dubious and have not been verified.

FLOWERING PERIOD: September--beginning of October.

HABITAT: Artemisia vallesiaca is considered to be a steppe relict of eastern origin. A number of species of similar phytogeographic origin form together with A. vallesiaca the association Artemisietum vallesiaceae on south- and southwest-facing slopes at 800--1000 m altitude in the valleys of the Rhône River and its affluents in Valais and in the Aosta valley of Piemonte, which are characterized by a hot arid climate. The substrate is generally a calcareous moraine, but occasionally the species may also be found in rock crevices.

In a poor form of the association several lichens are found, together with grasses, e.g., Festuca vallesiaca and Poa bulbosa. Often the association is very rich in herbs as well as grasses, however, above all members of the Koelerietum vallesianae, e.g. Ephedra helvetica, Koeleria vallesiana, Stipa capillata and pennata, Carex nitida, Asperula cynanchica, Odontites lutea and Onosma helvetica. Very often Prunus spinosa, Dianthus carthusianorum and Artemisia campestris are found scattered in the Artemisietum vallesiaceae. In Italy the association in a few localities includes the great rarity



Kochia prostrata.Localities

SWITZERLAND. Valais. Near Ardon (G). -- Baltschieder, c. 680 m (LD). -- Brangon (E, G, JE, LD, UPS). -- Chippis, entrance of Val d'Anniviers (G). -- Conthey c. 1000 m SE, above Pont de la Morge, c. 570 m (LD). -- Fully (E, FI, G, HAL, JE, LD, LY, M, S, UPS, W, WU). -- Gampel, c. 670 m (LD). -- Granges c. 1000 m NE, near Clément, c. 550 m (LD). -- Granges c. 1000 m NW, along the road to Lens (JE, LD, W, WU). -- Leuk, c. 750--900 m (G, JE, K, W). -- Near Martigny (G, W). -- Below Nax, entrance of Val d'Hérens, c. 1050 m (FI, W). -- Raron, c. 620--670 m (LD, M). -- Saillon, c. 560 m (E, FI, G, HAL, JE, K, LD, S, UPS, W). -- Saillon c. 1400 m WNW, c. 550 m (LD). -- St. Léonard, c. 510 m (G, LD, LY, W). -- Salgesch (FI, G). -- Near Sierre, c. 600-700 m (FI, G, JE, K, LD, LY, S, W). -- Between Sierre and Varen (E). -- Sion c. 1500 m NE, Champlan, c. 800 m (FI, G, M, S). -- Near Sion, Montorge (FI, G, HAL, JE, M, S, W). -- Sion, Tourbillon, c. 700 m (E, FI, G, JE, K, LD, LY, M, S, UPS, W, WU). -- Sion c. 1500 m WSW, c. 550 m (LD). -- Between Sion and Sierre, on "La Plâtrière" hill (FI, W). -- Val d'Hérens, between St. Martin and Bramois (G). -- Vallée de Bagnes, at Weisshorn (G). -- Between Varen and Leuk (E, HAL, G, LD). -- Visp, c. 700 m (M). -- Zermatt (JE, LD).

ITALY. Piemonte. Valle d'Aosta: Aosta, near the railway station, c. 575 m (M); Aosta, the hill of Gargantua, c. 700--800 m (FI, G); Aymaville (FI); Brissogne (FI); Chambave (FI); Between Chambave and Champlan (FI); Between Chambave and Nus (FI); Courmayeur (G); S. Nicolas (FI); Sarre, c. 620 m (LD); Villeneuve, c. 690 m (FI, G, LD). -- Valle di Cogne, Ponte d'El (FI). -- Val Peltine, Doues (FI).

ARTEMISIA SANTONICUM L.

Linnaeus 1753 p. 845. -- Original collection: without locality (LINN no. 988:11, large specimen on right, lectotype selected by Leonova 1969).

A. monogyna Waldstein-Wartemberg & Kitaibel 1802 p. 77 tab. 75.  
 -- A. maritima L.  $\eta$ . monogyna (Waldst. & Kit.) Ledebour 1845 p. 573 (superfluous when published as A. maritima L. O. kitaibeliana Besser was cited as synonym). -- A. santonicum L. var. monogyna (Waldst. & Kit.) Fritsch post a. 1893 no. 2265:I (superfluous when published as A. maritima L.  $\alpha$ . erecta Neilr. was cited as synonym).  
 -- A. salina Willd. ssp. monogyna (Waldst. & Kit.) Sagorski 1907 p. 16. -- A. maritima L. ssp. monogyna (Waldst. & Kit.) Gams in Hegi 1928 p. 664. -- A. santonica L. ssp. monogyna (Waldst. & Kit.) Leonova 1969 p. 363. -- Original collection: Hungary, Tisza (PR no. 495744 a, left specimen on sheet, lectotype).

A. maritima L. O. kitaibeliana Besser 1834 p. 40. -- Original collection: USSR, Odessa (S, Herb. Bess., lectotype).

A. maritima L.  $\alpha$ . erecta Neilreich 1859 p. 353. -- Original collection: Austria, Baumgarten, 15.9.1853 (W, Herb. Neilr., lectotype).

A. maritima L.  $\beta$ . patens Neilreich 1859 p. 353. -- A. salina Willd. ssp. patens (Neilr.) Sagorski 1907 p. 15. -- Inquires about original material have been unsuccessful. Description and distribution confirm the synonymy. Neotype: Austria, "Goys am Neusiedler See", 18.9.1853. Leg. J. Junatzká (W).

A. praticola Klokoy 1962 p. 345. -- Description and distribution confirm the synonymy (cf. Leonova 1970).

A. pseudofragrans Klokoy 1962 p. 342. -- Description and distribution confirm the synonymy (cf. Leonova 1970).

Illegitimate synonym: A. pendula (Schur) Schur 1860 p. 228 (later homonym of A. pendula Salisbury 1796 p. 191). First described as a variety of A. maritima L. in Schur 1853 p. 39.

Note: A. santonicum L. was still cited by Stechmann (1775 p. 25) and Willdenow (1803 p. 1826), but the name has since then been rejected in most floras, mostly because of the former use of the species name ("Santonicum") for a number of medicinal herbs of the subgenus Seriphidium and the consequent uncertainty which plant Linnaeus had in fact described (the type material was not consulted). Waldstein & Kitaibel evidently at first accepted the species as occurring in Hungary, as it was listed in the preface of their "Icones" (1799



p. XXXI), however, later in the same work (1802) they omitted the species (but described their own species A. monogyna). After the publication of this work the taxon was generally called A. monogyna Waldst. & Kit. in floras and herbaria, or else it was confused with either of Willdenow's two species (1803) A. salina (see p. 101) and A. nutans. Fritsch was one of the few authors to accept A. santonicum L., and it was included in the first edition of his "Exkursionsflora" (1897 p. 577), but in the second edition (1909 p. 626) he had changed the name in favour of A. monogyna Waldst. & Kit. Leonova (1969) was evidently the first author to study the type material, and she identified this as a Russian species, conspecific with A. monogyna Waldst. & Kit. of the Pannonic area. The present author has arrived at the same conclusion after studying the type material.

ILLUSTRATIONS: Figs. 113--115 (habit), 112 (distribution).

A suffrutex with a moderately branched, horizontal--ascending rhizome, c. 2--5 mm in diam., with usually smooth surface, often reddish. Internodes c. 5--20 mm long. A moderate production of sterile rosette-bearing shoots. -- Stems ascending, c. (15--20--50(--60) cm long, moderately(--strongly) suffrutescent, sparsely--moderately pubescent (greyish-green--grey) at first but soon glabrous especially at the base, often becoming reddish--brownish; moderately branched, usually from or below the middle, not seldom from the base. Branches of very varying but usually moderate length, c. 2--10(--20) cm, erect or distally pendent (seldom wholly pendent). -- Lower cauline leaves distinctly petioled, sometimes auricled, sparsely--moderately pubescent (dull green--greyish), soon dropping off. Laminae c. 10--35(--45) mm x 7--20(--25) mm, 2--3-pinnatisect, with linear(--slightly spatulate) segments c. 0.4--0.8(--0.9) mm broad, acutely--subacutely apiced. Leaves on sterile shoots similar but segments often broader and more spatulate. Upper cauline leaves increasingly simple, uppermost very small, pinnatifid or entire. Stomatal cells c. 16--40  $\mu$  long. -- Hairs on stems, branches and leaves T-shaped, with long arms, two or three basal cells. Glands c. 35--50  $\mu$  at broadest part (middle--top), each gland consisting of eight secreting cells in two rows and two basal cells; present on all aerial parts (except achenes). -- Synflorescence rather lax (--moderately compact), seldom secund, with almost sessile--fairly

long-stalked capitula on panicle branches of (primary--secondary order. -- Capitula erect or pendent, oblong--elliptic, c. 2--4.5 (5) mm long, with peduncles c. (0--0.5--4--10) mm long. -- Phyllaries in rather close, imbricate arrangement, acute--subacute (blunt), glandular; outer very small, triangular, largely herbaceous, very sparsely pubescent; inner oblong--elliptic (obovate), c. 2.5--3.8 (4.0) mm x 0.9--1.6 (1.8) mm, glabrous except for glands (seldom sparsely pubescent), with scarious margins c. 0.2--0.6 mm broad, herbaceous midrib region often with red margins, linear or tapering to an acute--subacute apex. -- Florets c. (1--2--6, all hermaphrodite. Corolla c. (1.9--2.0--2.8 mm long, reddish or yellow, glandular, tubular, widening slightly in the upper part; corolla lobes 5, rather narrowly triangular, c. (0.30--0.35--0.50 (0.55) mm long. Corolla length/lobe length ratio c. (4.5--5.0--7.0 (7.5)). Anthers c. 0.8--1.2 mm long, acutely appendaged basally; apical appendage narrowly lanceolate, c. 0.20--0.35 (0.40) mm long, acute. Pollen grains tricolporate, c. 14--30  $\mu$  in diam. Style longer or shorter than corolla tube, style branches flattened, c. 0.4--0.7 mm long. -- Achenes narrowly obovate, c. 1.5--2.1 (2.2) mm x 0.7--0.9 (1.0) mm, with low longitudinal ridges c. 40--80  $\mu$  broad. Style scar usually oblique, sometimes surrounded by a low bulge. -- Chromosome number  $2n=18, 36, 54$ .

A very variable species, especially as regards the branching system. Leonova (1969 pp. 362--363) divided A. santonicum into two subspecies, viz., ssp. santonicum and ssp. monogyna (Waldst. & Kit.) Leonova. For the first-mentioned subspecies Leonova stated the area of distribution as the USSR and Roumania, and "possibly some specimens from the Tisza area in Hungary can also be classified as ssp. santonicum". Ssp. monogyna was stated to occur in Hungary, Czechoslovakia and Austria. The present author has shown that there are three cytotypes within A. santonicum, with only diploids occurring in Austria and Czechoslovakia, only polyploids in eastern Roumania, Bulgaria, Greece and the USSR, and both diploids and polyploids in Hungary, Yugoslavia and western Roumania. Furthermore, the author has considered it appropriate (for reasons discussed on pp. 73--75) to subdivide the species into two subspecies. These subspecies were established as having many more or less intermediate forms in the area where they meet (Hungary--western Roumania). So far, the results coincide fairly well with Leonova's observations. However,



an examination of the type material of A. santonicum L. and A. monogyna Walldst. & Kit. showed that both type specimens are polyploid. The outer morphology and measurements of the A. santonicum type are typical of a polyploid, whereas the A. monogyna type is more intermediate but still undoubtedly polyploid. Thus, the pollen grains are approximately  $22\ \mu$  in diam. Through her choice of type material, Leonova's division of the species confuses the natural relationships within the taxon. One of her subspecies will comprise morphologically more or less similar diploids and tetraploids, while the other subspecies will comprise the rest of the tetraploids (and hexaploids?). In the present author's opinion, all tetraploids should instead be placed within one subspecies, as they are very probably only segregates of the same (probably segmental) allopolyploid. For reasons stated on p. 74, the hexaploids may also be included with the tetraploids in the same subspecies, while the diploids should be treated as a separate subspecies, a subspecies that on the whole is morphologically easy to distinguish and that is also reproductively isolated from the rest of the species. The following subdivision of the species A. santonicum L. is therefore suggested:

Artemisia santonicum L. ssp. santonicum

Bibliography and synonymy as under the species, excluding A. maritima L.  $\alpha$ . erecta Neilreich and A. maritima L.  $\beta$ . patens Neilreich (A. salina Willd. ssp. patens /Neilr./ Sagorski).

ILLUSTRATIONS: Figs. 113, 114 A.

Rhizome usually c. 3--5 mm in diam.. -- Stems sparsely--moderately pubescent, usually more pubescent and more seldom reddish in the eastern part of the area of distribution, c. (15--)30--50 (50--60) cm. Branches more often pendent than erect. -- Laminae of lower cauline leaves c. (15--)20--35(--45) mm x (10--)15--20(--25) mm, with leaf segments c. 0.5--0.8(--0.9) mm broad. Breadth of leaves (if entire) or middle segment of leaves in upper half of

synflorescence c. (0.5--0.6--0.8(--1.0) mm. Stomatal cells c. 25--40  $\mu$ . -- Glands c. 40--50  $\mu$  at broadest part (middle--top). -- Capitula c. 3--4.5(--5) mm long, more often elliptic than oblong. -- Inner phyllaries c. (0.9--1.2--1.6(--1.8) mm broad, herbaceous midrib region sometimes with red margins (mostly in the western populations); scarious margins c. 0.3--0.6 mm broad. -- Florets c. (2--3--6. Corolla c. (2.2--2.3--2.8 mm long, reddish or yellow; corolla lobes c. (0.35--0.40--0.50(--0.55) mm x 0.30--0.45 mm. Anthers c. (0.9--1.0--1.2 mm long; apical appendage c. 0.25--0.35(--0.40) mm long. Pollen grains c. 19--30  $\mu$  (usually c. 21--25  $\mu$ ) in diam. Style branches c. 0.5--0.7 mm long. -- Achenes c. (1.5--1.8--2.1(--2.2) mm x 0.8--0.9(--1.0) mm. -- Chromosome number  $2n=36, 54$ .

**DISTRIBUTION:** On solontschak and solonetz soils in inland marshes, depressions and salt-meadows of steppe and semi-desert areas in Hungary, Yugoslavia (a few localities near the Hungarian and Roumanian borders), Roumania, Bulgaria, Greece (Thraci), Turkey (European part), and the USSR (southern European part and, according to Leonova, also Ciscaucasia and Dagestan).

**FLOWERING PERIOD:** September--October.

**HABITAT:** A. santonicum ssp. santonicum in the Pannonic region (Hungary, western Roumania, Yugoslavia) usually occurs in alkali areas climatically determined by a low rainfall. Two major types of soils are prevalent in these areas, viz., solontschak and solonetz soils. The solontschak (white alkali) soils are rich in chalk and sodium chloride, and often also rather sandy. The salt usually accumulates in the surface layers. Ssp. santonicum generally occurs on slight elevations together with scattered species from surrounding associations, e.g. Puccinellia distans ssp. peisonis or ssp. limosa, Festuca pseudovina, Lepidium cartilagineum, Plantago maritima and Aster tripolium ssp. pannonicus.

In the solonetz or black alkali soils the water-table is usually low, and the salts, dominated by sodium carbonate, accumulate at some depth below the surface. These soils are poor in chalk and often silty. Ssp. santonicum occurs in a zone just below a Festuca pseudovina society and often together with Limonium gmelinii. Some species from the surrounding zones occur scattered in the Limoniето-Artemisietum, e.g. Puccinellia distans ssp. limosa, Festuca pseudovina, Camphorosma annua, Plantago tenuiflora and Centaurea jacea ssp. angustifolia ("C. pannonica").



The Roumanian marshes, above all around the Danube and its affluents, are often less arid, and ssp. santonicum here occurs also at somewhat lower levels, often in an association dominated by Halimione verrucifera and with Aster villosus as another subordinate species. At the higher levels the codominants are still Campylopus annuus and Limonium gmelinii, for example.

Along the coasts of the Black Sea ssp. santonicum frequently grows on saline slopes on more or less clayey or sandy soils. Further eastwards, in the southern part of European Russia, the climate is often arid and the habitats of the subspecies are mostly of a steppe or semi-desert type, with solontschak (more humid) or solonetz soils as substrates. However, in this area, too, ssp. santonicum may be found outside the steppe regions, e.g. in depressions of salt-meadows and on saline river banks and slopes.

In Greece ssp. santonicum has its only localities (known to the author) in Thraki, around Lake Vistonis. Large areas are here covered by a halophytic vegetation. The soil is rather sandy and dries out during the summer. The subspecies usually grows in a belt above a zone dominated by species of the Chenopodiaceae, e.g. Arthrocnemum glaucum and Halocnemum strobilaceum. Limonium vulgare and, mostly, Halimione portulacoides codominate in the Artemisietum.

Artemisia santonicum L. ssp. patens (Neillr.) K. Persson comb. nov.

A. maritima L.  $\beta$ . patens Neillreich 1859 p. 353. -- A. salina Willd. ssp. patens (Neillr.) Sagorski 1907 p. 15. -- Original collection: Austria, "Goys an Neusiedler See", 18.9.1853. Leg. J. Jüratzka (W, neotype).

A. maritima L.  $\alpha$ . erecta Neillreich 1859 p. 353. -- Original collection: Austria, Baumgarten, 15.9.1853 (W, Herb. Neillr., lectotype).

Note: A. salina Willd. ssp. patens (Neillr.) Sagorski was published as a name for forms of A. salina from Artern, Germany. The name was really superfluous as A. salina Willd. was cited as a synonym (the name should be A. salina Willd. ssp. salina), but it is not illegitimate because Neillreich's basionym was legitimate (cf. Art. 63,

International Code of Botanical Nomenclature, Utrecht 1972). When published the name was incorrect, but it will become correct in a new combination under A. santonicum L., as this taxon and A. salina Willd. are treated as different species.

ILLUSTRATIONS: Figs. 114 B, 115.

Rhizome usually c. 2--3 mm in diam. -- Stems sparsely(--moderately) pubescent, often reddish--brownish, c. (15--20--40(--50) cm. Branches more often erect than pendent. -- Laminae of lower cauline leaves c. 10--20(--25) mm x 7--15 mm, with leaf segments c. 0.4--0.6(--0.7) mm broad. Breadth of leaves (if entire) or middle segment of leaves in upper half of synflorescence c. 0.3--0.6(--0.7) mm. Stomatal cells c. 16--29  $\mu$  (usually less than 25  $\mu$ ). -- Glands c. 35--40  $\mu$  at broadest part (middle), usually more rounded than in ssp. santonicum. -- Capitula c. 2--4 mm long, more often oblong than elliptic. -- Inner phyllaries c. 0.9--1.4(--1.5) mm broad, herbaceous midrib region often with red margins; scarious margins c. 0.2--0.5 mm broad. -- Florets c. (1--2--4(--5)). Corolla c. 1.9--2.4(--2.5) mm long, mostly reddish; corolla lobes c. 0.30--0.45(--0.50) mm x (0.25--0.30--0.40(--0.45) mm. Anthers c. 0.8--1.0 mm long; apical appendage c. 0.20--0.30 mm long. Pollen grains c. (14--17--20  $\mu$  in diam. Style branches c. 0.4--0.6(--0.7) mm long. -- Achenes c. 1.5--1.9(--2.0) mm x 0.7--0.9 mm. -- Chromosome number  $2n=18$ .

DISTRIBUTION: On solontschak and solonetz soils in inland marshes, depressions and salt-meadows in the lowlands of the Pannonic region, i.e. Austria (Neusiedler See area), Czechoslovakia (southern Slovakia), Hungary, Yugoslavia (near the Hungarian and Roumanian borders) and Roumania (Timișoara--Arad--Oradea area).

FLOWERING PERIOD: September--October.

HABITAT: In Hungary and western Roumania ssp. patens occurs together with ssp. santonicum in several localities. The localities of the Neusiedler See area and southern Slovakia are mostly very similar to those in the rest of the Pannonic region. The soils are either of the solontschak or the solonetz type, and the climate is arid, so the latter type of soil in particular generally dries out in the summer with resultant high salinities. On the solontschak soils ssp. patens usually grows together with Puccinellia distans ssp. peisonis, Lepidium cartilagineum and Plantago maritima, whereas



Puccinellia distans ssp. limosa, Festuca pseudovina, Camphorosma annua and Plantago tenuiflora are most typical for the Artemisietum on solonetz soils. Several of the associated species, e.g. Lepidium cartilagineum, Camphorosma annua and Puccinellia distans ssp. limosa, reach their western boundary in the Neusiedler See area, as does Artemisia santonicum.

### Localities

#### Only ssp. santonicum

HUNGARY. Békés. Gyula, Kispéli legelő (S). -- Borsod-Abaúj-Zemplén. Szerencs, Legyes-Bénye (W). -- Tokaj (W). -- Hajdu-Bihar. Near Debrecen (LD). -- Hortobágy-Máta (LD). -- Nagyhortobágy (LD, M, S). -- Jász-Nagykun-Szolnok. Szolnok (W). -- Pest. Abony (WU). -- Nagykáta, Tó-Almaş (L, WU).

YUGOSLAVIA. Vojvodina. Apatin (PR). -- Bezdan (PR). -- Horgoš (PR).

ROMANIA. Bucureşti. Comana (LD, LY, W). -- Ialomiţa, Siliştea-Cotorca (W). -- Vidra (FI). -- Cluj. Apahida (G, JE, LD, M, W, WU). -- Apahida, Búdös tó (CL). -- Cluj (W). -- Near Cluj: Dezmér (CL); Fânate (G); Hoia (FI); Şanţu turcului (G); Someşeni (LD); Török-vágás (G, LD, M). -- Cojocna (CL, G, K, LD, W, WU). -- Gherla (G). -- Between Sic and Gherla (FI, WU). -- Turda (CL, E, FI, G, JE, K, L, LD, M; PR, W, WU). -- Turda, Báile Sárate (CL). -- Valaszut, on the river Someşul-Mic (W, WU). -- Constanta. Dobruja: Babadag (LD); Constanta (W). -- Craiova. Dolj, near Bratovoesti (M). -- Galati. Dobruja, Tulcea (LD). -- Hunedoara. Mercurea NW, Koncza (FI, LY, W, WU). -- Iaşi, Cîrlig, Sărătura (M). -- Cucuteni, Val. Bahlui (CL). -- Oraşul-Stalin. Hóldvilág (Abtsdorf) (JE, K, M, PR, WU). -- Ocna-Sibiului (Salzburg) (FI, JE, LY, M, S, UPS, W, WU). -- Ploesti. Buzău: Beceni (LY); Berca (CL). -- Timişoara. Near the road between Timişoara and Recaş (JE, M, W).

BULGARIA. Burgas. Near Burgas, salines (JE, S, UPS). -- Near Burgas, Vajakrei (FI). -- Stara Zagora. Kermen, Giola (SOM). -- Radnevo, Solenata (SOM). -- Tolbuhin. Cape Kaliakra (M).

TURKEY. Canakkale. Gelibolu, Büyük Kemikli Burun (Cape Suvla) (K).

GREECE. Thraki. Xanthi: Akr. Baloustra (K); Porto Lago, shores of Lake Vistonis (K); Porto Lago c. 4000 m WNW (LD).

USSR. Ukrainskaya SSR. Kuyalnikskii Liman (FI). -- Odessa (E, FI, JE). -- Tiligulskii Liman (WU). -- Kharkov, Starobelsk (S). -- Krym: Isunj (LE); Nižnegorskii (LE). -- Mariupol, on the Sea of Azov (M). -- Rossiiskaya SFSR. Astrakhan (K). -- Čerkassk (S). -- Krasnoarmeisk (Sarepta) (FI, JE, LD, LY, S, UPS).

Both ssp. *santonicum* and ssp. *patens*

HUNGARY. Bács-Kiskun. Kalocsa: Hajós (FI, G, K, LY, S, WU); Homokméggy (FI, L?, M, PR). -- Jász-Nagykun-Szolnok. Kisújszállás (HAL, K, M, PR, S, UPS, WU). -- Kunhegyes (G, PR).

YUGOSLAVIA. Srbija. Vršac (PR, W).

ROUMANIA. Arad. Chişineu (G, PR, S).

Only ssp. *patens*

AUSTRIA. Burgenland. Gols (UPS, W, WU). -- Seewinkel: Lacke east of Apetlon (M); Apetlon c. 1500 m E, Mosadolacke (M); Apetlon E, Silberlacke (M); Apetlon c. 1500 m NNE, southern part of Xixsee (LD); Apetlon c. 2000 m NE, eastern part of Xixsee (LD); Illmitz c. 1200 m E (LD); Illmitz W, Kirchsee (M); Langelacke, south-western corner (G, LD, M, WU); Oberstinkersee (LD); Sandy shore near Podersdorf (LY, M, PR, W, WU); Podersdorf c. 3000 m SE (LD); Between Podersdorf and Illmitz (S); Between Weiden and Podersdorf (JE); Between Xixsee and Langelacke (LD). -- Niederösterreich. Marchfeld, Baumgarten (E, FI, G, JE, K, LD, M, UPS, W, WU).

CZECHOSLOVAKIA. Slovensko. Bratislava NE: Svätý Jur (FI, LD, M, PR, PRC, S, WU); Svätý Jur SE, Šúr (PRC); Between Svätý Jur and Vajnory (PRC). -- Nitra: Between Štúrovo (Parkán) and Kamenné Ďármoty (PRC); Between Štúrovo (Parkán) and Kamendín (E, M); Štúrovo (Parkán) (FI, LD, M, K, W, WU); Nové Zámky NW, Palárikovo (LD); Kamenné Ďármoty (L, W, WU); Kamendín (FI, G, LD, M, S, UPS, W, WU).

HUNGARY. Bács-Kiskun. Kunszentmiklós (E, FI, G, JE, LD, M, PR, S, W, WU). -- Fejér. Pákozd (W). -- Dinnyés on Velencei Tó (W, WU). --



Szűnyogpuszta (FK). -- Győr-Sopron. Györszemere (S). -- Magyaróvár (W). -- Hajdu-Bihar. Near Püspökladány, Szerep (JE). -- Between Püspökladány and Szentágotai Csárda (WU).

ROUMANIA. Arad. Șimand (JE).

Not referable to subspecies

HUNGARY. Békés. Békés (LD). -- Pest. Tápiószele (E, W).

ROUMANIA. Arad. Kéthulom (M). -- Oradea. Salonta, between the town and the river (CL).

## PART II. COMMENTS ON VARIATION AND EVOLUTION WITHIN THE COMPLEX

### THE KARYOTYPE

In the three species subjected to analysis in the first part of this investigation, viz., Artemisia maritima, A. vallesiaca and A. santonicum, the basic number of  $x=9$  was found in all cases. The same basic number was also established for two other species within the complex, viz., A. gallica from the south coast of France (11 populations) and A. caerulescens from Portugal (5 populations) and Istra, Yugoslavia (2 populations). All populations were found to be diploid,  $2n=18$  (Fig. 116), which confirms previous counts by, for instance, Martinoli (XIth International Botanical Congress, Seattle 1969) on French (A. gallica) and Italian (A. caerulescens) material.

From the other species within the complex no spontaneous material has been available to the author. For some of them, chromosome numbers (all with  $x=9$ ) have been published by other authors (Table 20), but as for most reports on other species within this taxonomically complicated group, it is difficult to verify the correctness of the taxonomic determinations. One way to get at least some idea of the ploidy level is to measure the pollen grains of the respective species, keeping in mind that the correlation between pollen size and ploidy level is absolute only for closely related taxa and less reliable for species more distantly related. The present author measured pollen grains from pressed material of Russian origin of A. lerchiana, A. taurica, A. nitrosa, A. fragrans and A. pauciflora (Table 20), the taxonomic determinations having been made either by the author or by Leonova. If the pollen measurements are compared with similar measurements for taxa where the chromosome number has been determined by the author, it can be seen that A. pauciflora is probably diploid, while A. lerchiana and A. fragrans may be polyploid, possibly tetraploid. For the two last species a diploid number has also been reported, and diploids may well exist, though the present author has not seen any herbarium material that is definitely diploid, at least not based on pollen size. It is to be noted that the species apparently most closely related to A. lerchiana,



vis. A. vallesiaca, is tetraploid. Both a tetraploid and a diploid number have been reported for A. taurica. Another species showing affinity with A. ierchiana. The pollen measurements in the present investigation indicated diploidy, though tetraploidy cannot be excluded. A. nitrosa is either diploid or tetraploid. In conclusion it may be stated that diploids probably comprise a somewhat smaller proportion than polyploids within the complex.

The basic number of  $x=9$  seems to dominate not only in the genus Artemisia as a whole (Suzuka 1950, 1952; Arango 1962, 1963, 1964; Kiviatari & Ojano 1964) but in most Anthemideae, e.g. Anthemis (Hartling 1950) and Achillea (Threudorfer 1964 b). Anthemis is dominated by diploids, but Achillea, though entomophilous, is rather like Artemisia in many respects, for instance, in the occurrence of several polyploid complexes with reticulate patterns of relationships. In Artemisia such complexes have been subjected to detailed investigation by, for instance, Yeck 1946 (A. vulgaris aggregate in North America), Ward 1953 (section Seriphidium in North America) and Threudorfer 1964 (chiefly Heterophyllae of the section Artemisia). In all these complexes both diploids, tetraploids and hexaploids were found, though in varying proportions and at varying levels of morphologic differentiation. Thus in the Heterophyllae the polyploids dominate, and each taxon comprises only one cytotype, i.e. the polyploids are morphologically highly differentiated and easily recognizable. In the A. vulgaris complex (North America) the polyploids also dominate but to a lesser degree, and one of the eight taxa investigated comprises both tetraploids and hexaploids (cf. A. santonicum ssp. santonium). The section (subgenus) Seriphidium in North America is perhaps more interesting as far as the present investigation is concerned, as it is probably more closely related to species dealt with in this investigation. It seems that it is also cytotaxonomically more like these species. Of the twelve taxa investigated by Ward, six were both diploid and tetraploid, one comprised tetraploids, hexaploids and even octoploids. And five were either diploid (four taxa) or tetraploid (one taxon).

It is a strange fact that an advanced condition such as dysploidy occurs in all subgenera of Artemisia except Seriphidium, which is otherwise considered to be the most advanced subgenus apart from Pracuncululus (Hall & Clements 1913). No record of  $2n=16$  or of stable  $2n=34$  or  $52$  (possibly products of dysploid/euploid unions) have ever been published for species within Seriphidium, and these (stable) numbers have not been observed by the present author either. However,

more unstable variations in chromosome number, such as aneuploidy and aneusomy, have been found also in Scirpoidium. Thus, occasional aneuploidy was observed by Ward (1933) in A. rothrockii ( $2n=53$ , 54) and in this investigation in A. santonicum ssp. santonicum ( $2n=38$ , 39) and A. maritima ( $2n=30--33$ ). Only one record of aneuploidy exists from other subgenera, viz., A. montana (subgen. Artemisia) with  $2n=41$ , 42, 43, 44 (Goloborodov 1947), but in the present author's opinion the phenomenon is probably not uncommon (though attention has not been paid to it) in polyploid perennials of the genus (cf. polyploid Achillea species, Erendorfer 1953).

The very unstable cytologic condition of aneusomy, such as observed in A. maritima in the present investigation, does not seem to have been recorded elsewhere in the genus (A. montana may be a possible case, as Goloborodov does not mention whether the numbers observed originate from one or separate individuals). Intra-individually varying chromosome numbers are reported in other Anthemideae, however, viz. in Achillea (the Millefolium complex, Erendorfer 1953 a, b), but in this case the variation occurs only in diploids, in generative tissue only, and there is generally an increase in chromosome number (in Artemisia maritima mostly a decrease). The intra-individually aneuploid Artemisia and Achillea species evidently fall within separate groups of those described by Erendorfer (1953 a) (see p. 15).

The morphology of the chromosomes is fairly similar throughout the genus (cf. Agave 1942, 1943, 1944; Erendorfer 1944). The chromosomes are only slightly different in size, usually varying between 2 and 3  $\mu$  for the shortest and between 4 and 5  $\mu$  for the longest ones. Most of the chromosomes in a set are metacentric or submetacentric, but there is always a group of distinctly asymmetric chromosomes with subterminal centromeres. If the diploids are compared it can be seen, as in Achillea (Erendorfer), that the number of subtelocentric chromosomes is not the same in all taxa. In Heterophyllae (Erendorfer) and other groups (Agave) there are usually two or three pairs of such chromosomes, and this is also the case in the A. maritima complex. Thus, A. santonicum ssp. patens from Austria has two pairs of asymmetric chromosomes, while the same taxon from Czechoslovakia seems to have three pairs (Fig. 14 A--C). The same conditions are found in the A. gallica--caerulescens group, in that A. gallica from France and A. caerulescens from Portugal in their highly similar karyotypes comprise two pairs of chromosomes



with subterminal centromeres, while A. caerulescens from Yugoslavia has three pairs in the otherwise similar chromosome set (Fig. 117). Such cases may be the result of structural rearrangements, e.g. translocations.

Satellites are often found on the subtelocentric chromosomes, the number varying but generally increasing with the ploidy level. According to Ehrendorfer (1964) only one satellite pair per genome is found in Heterophyllae, but in several other groups of the genus Masumori (1961) found two satellite pairs in many diploids. Arano never found more than one satellite pair per genome in his investigations (partly the same species as in Masumori's study), except in one dysploid species ( $2n=16$ ), A. fukodo (Arano 1963), which had two pairs. The variation in satellite number may be the result of different preparation techniques, but it may also be real as the satellites, at least in the A. maritima complex, have been observed by the present author to be highly varying both in number, size and position (sometimes also long chromosome arms are satellited, Fig. 14 D), and both within and between populations. A certain geographical pattern of satellite variation is often evident, however. Thus, A. maritima has up to 10 satellites in some regions, but only up to four in other regions, while in some instances there appear to be no satellites at all. In A. caerulescens from Portugal and A. gallica from France about 50 % of the individuals investigated have four satellites (Fig. 117) but in the Yugoslavian A. caerulescens only c. 25 % (and the fourth satellite is seen only faintly).

Heterozygosity for satellites, either in number or size, also seems to be fairly common, at least in the A. maritima complex, where it has been observed in all species investigated. Thus, in some instances A. caerulescens and A. gallica have three satellites, and both in this and other cases the satellites are often all of a different size. Some plants of Hungarian A. santonicum ssp. santonium are heterozygotic for a very distinct secondary constriction cutting off two thirds of a long chromosome arm (Fig. 14 D). On the whole, it seems that satellites are unreliable chromosome markers in Artemisia, as in a number of other perennial angiosperms, e.g. Leopoldia (Bentzer 1969, 1972) and Bellevalia (Bentzer, Bothmer & Wendelbo 1972).

As regards the morphology of the genomes contained in the polyploid species, it seems that there are generally not two (in tetraploids) or three (in hexaploids) exactly similar genomes per set either in Heterophyllae (Ehrendorfer 1964), Seriphidium (the pre-

sent investigation) or other groups of Artemisia (Arano 1962, 1963, 1964). According to Ehrendorfer (and it is also the present author's opinion) these conditions indicate a hybridogenic origin of the polyploids (allopolyploidy).

#### MORPHOLOGIC VARIATION

Artemisia is an extremely polymorphic genus. Much of this polymorphism is a consequence of the many polyploid complexes within the genus. Each complex consists of two or mostly more diploid species as a basis in a complicated pattern of polyploids of different levels reticulately related to one another. The extreme polymorphism of the polyploids is the result of extensive recombination of the diploid parental characters, which in many cases in themselves are very variable. The boundaries between the ploidy levels are often more or less diffuse owing to such recombination and segregation towards one or both of the parents, and also because of introgression in localities where two cytotypes meet. In some groups of the genus, for instance, the Artemisia vulgaris complex in North America (Keck 1946) and even more in the Heterophyllae of the subgenus Artemisia (Ehrendorfer 1964), the different cytotypes are mostly well differentiated morphologically and therefore fairly easily recognizable. Moreover, the diploid parents are apparently in many cases extinct. Within other groups of the genus such as the Seriphidia of North America (Ward 1953) and Europe, and also in other genera within the Anthemideae, e.g. the Achillea millefolium complex (Ehrendorfer 1959 b), the taxonomic problems are greater as there is a great deal of overlapping between different cytotypes and many specimens can be determined only with difficulty. In a number of localities diploids and polyploids occur together with consequent introgression, probably via unreduced gametes of the diploids. Ward reported all plants intermediate between diploids and tetraploids to be tetraploid, and he found no triploids. The same conditions are probably prevalent in



the area where the diploid Artemisia santonicum ssp. patens and the tetraploid A. santonicum ssp. santonicum meet. Such overlapping of morphological characters in different cytotypes makes taxonomic classification of those cytotypes in many cases highly impracticable, at least at species level. Sometimes, however, such as in the case of A. santonicum, subspecific rank is warranted on account of the largely vicarious distribution and as at least a majority of the allopatric populations are fairly easy to recognize morphologically.

Much of the morphological variation in Artemisia is apparently hereditary, as can be established after cultivation under uniform conditions, but in addition there is also a great deal of modificative plasticity which often tends to obscure the genetic differences. Thus, Ward (1953) reports that the cytotypes which are mostly indistinguishable in nature in cultivation will develop definite size differences. Within A. maritima ssp. maritima the ecotype from western Sweden (Bohuslän--Halland) is mostly fairly typical in cultivation, but in nature it is not sufficiently distinct as to make it easily recognizable on herbarium sheets, for instance, so that the use of a separate subspecific name for this ecotype is impracticable. Wendelberger (1960) established the following characters as being particularly apt to environmental modification in the group Heterophyllae: plant height, leaf size, leaf proportions (to a certain extent), breadth of leaf segment and degree (though not type) of segmentation. Much the same characters are modificative in the Artemisia maritima complex, above all shoot length and leaf size. The degree of leaf segmentation is more or less variable in different species of the complex. Thus the leaves of A. caerulescens and A. gallica are more alike in cultivation than in nature, the leaves of A. caerulescens becoming more segmented and those of A. gallica becoming larger with sparser segmentation. According to Beguinet (1908) and Milhofer (1933) the degree of leaf segmentation is a character of only slight taxonomic importance in A. caerulescens as it is influenced by the salinity and moisture of the substrate. Plants with entire leaves can thus be found in the most saline localities. A. lerchiana is also reported to vary in leaf morphology owing to differences in moisture and salinity (Leonova 1970). Plants in less humid localities are mostly smaller-leaved and the leaves are more richly divided with shorter segments.

Other shoot characters are modificatively variable to a lesser

extent, e.g. degree of suffrutescence and pubescence. Most floral and inflorescence characters, however, seem to be fairly rigid and only slightly phenetically influenced by environmental conditions, e.g. the type of synflorescence (branch rigidity, position of capitula etc.) excluding the internode length and the degree of branching.

Distinguishing for the genetically determined morphologic variation in the A. maritima complex is the fact that the characters apparently often vary independently of each other. This "box-in-box" differentiation contributes to the great taxonomic difficulties within the group. However, in many cases combinations of characters, especially vegetative characters, are apparently of adaptive importance, and some ecotypes have differentiated into more or less characteristic and distinguishable races within the species. An example of this racial differentiation is A. maritima ssp. humifusa, the general habit of which is probably an adaptation to the special ecological conditions prevalent on Öland, Gotland and Saaremaa (and perhaps before its migration to this area the conditions prevailing in the steppe areas further southeastwards during the last period of glaciation).

Another aspect of morphological variation that confuses the taxonomic relationships is that there are examples of probable parallel differentiation especially of vegetative characters within different species. Thus; A. maritima in its only inland localities (Thüringen, central Germany) and A. santonicum are both distinguished by sparse pubescence, the stems soon becoming glabrous at least basally, and cauline leaves withering at anthesis (or even before). These characters may be of adaptive importance as the habitats of the two taxa are rather similar (but it may of course also indicate that A. santonicum is one of the parent species connected with A. maritima, though the present author considers this less likely).

Notwithstanding the extensive polymorphism within the A. maritima complex certain patterns of relationships will emerge with careful morphological study, preferably in combination with cytological observations. Thus, from the morphology alone it is apparent that A. vallesiaca and the Russian A. lerchiana, A. dzevanovskyi and A. taunica form an affinity group of their own. In fact these species have often been considered conspecific, either under the name of A. vallesiaca or as ssp. vallesiaca within A. maritima. Besser (1834) named A. vallesiaca and A. lerchiana "A. maritima  $\kappa$ . lerchiana  $\alpha$ . europaea" and "A. maritima  $\kappa$ . lerchiana  $\beta$ . rossica", respectively. These are



the two species most similar morphologically, but A. lerchiana is generally not so densely pubescent (older shoots are often more or less glabrous basally), the leaves are larger, have longer, narrower segments and are mostly not long persistent, and the capitula are sometimes pendent. These characters indicate a possible relationship between A. lerchiana and A. santonicum ssp. santonicum, perhaps a common diploid parent (both are polyploid), though it must be noted that some of the characters may also be the result of parallel differentiation. A. taurica varies even more pronouncedly towards A. santonicum in the stem and leaf characters cited for A. lerchiana, and besides it is generally richly branched with long branches, and the sterile shoots are few and fairly long as in A. santonicum (many and short in A. vallesiaca and A. lerchiana). A. dzevanovskiyi is a taxon split off from A. lerchiana by Leonova (1969) on account of its denser and more persistent foliage and pubescence, taller stature, broader leaf segments, larger capitula and different habitat.

Another affinity group within the complex comprises two species, viz. Artemisia santonicum and A. nutans, which have partly the same distribution but different habitats. A. nutans was described by Willdenow (1803) on material from cretaceous slopes on the Dnepr River. This type material is very like A. santonicum in many respects. The capitula are extremely small, but they are obviously not mature, and such capitula are often also found in A. santonicum shortly before anthesis. Perhaps A. nutans should rather be classified with the rank of subspecies within A. santonicum. Poljakov (1961) evidently considered the two species to be conspecific, as he cited A. nutans as a synonym under A. monogyna (A. santonicum), but Leonova (1970) maintains both species after having studied both the type material and spontaneous material on cretaceous substrate. The present author has studied too little material to be able to form a definite opinion.

A. fragrans, belonging mainly to the area of Asia Minor and Caucasus but extending into Russia, shows affinity both with the lerchiana group and with A. santonicum, although it is obviously more distantly related than the previously mentioned species and is also morphologically more characteristic and therefore more easily recognizable. Another equally characteristic Russian species, A. pauciflora, also has certain characters in common with A. santonicum, above all the narrow imbricate involucre and the glossy phyllaries, and it is sympatric with this species at least in the lower Volga

area.

The two Mediterranean species A. gallica and A. caeruleascens seem to be very closely related judging from both morphology and cytology. As was mentioned previously, the karyotypes are very similar, and in cultivation under uniform environmental conditions great similarities in morphology will also emerge. Thus, the differences in plant height generally found in nature (A. caeruleascens is usually taller) disappear, and the leaves also become more alike as discussed above. The synflorescence characters are very much alike in both species, except that A. gallica apparently never has pendent branches as occasionally found in A. caeruleascens. In view of all these similarities in both morphology and cytology specific rank can hardly be maintained. In order to test the reproductive isolation between the two taxa, crosses were performed between populations from France (A. gallica), Portugal and Yugoslavia (A. caeruleascens). The crosses were successful in all directions resulting in many hybrid achenes with high germination frequency (almost 90 %). The hybrid plants had a somewhat reduced pollen fertility (percentage stainable pollen: mean value 62 %, range of variation 48--78 %), but in one of the crosses (no. 142 x 44, France x Yugoslavia) F<sub>2</sub> plants were also produced. These results, in combination with conclusions from morphological and cytological studies, indicate that the two taxa are best treated as subspecies within one species. The following subdivision of the species Artemisia caeruleascens is therefore proposed:

Artemisia caeruleascens L. ssp. caeruleascens

Linnaeus 1753 p. 848. -- Original collection: without locality (BM, Herb. Cliffort., sheet no. 5, lectotype).

DISTRIBUTION: Portugal (south of Lisboa), Spain (south-western corner), France (Corse), Italy (north-eastern coast southwards to Bari; Toscana and Romagna also inland localities, var. cretacea Flori; Sardegna), Yugoslavia (mostly on the north-western coast), Albania.

Flowering shoots c. 20--60 cm. Leaves on lower third of stem entire (lanceolate--linear) or sparsely pinnatifid--pinnatisect with primary segments usually about 5--15 mm long, ultimate segments on



pinnatisect leaves elongate, usually more than 0.7 mm broad. Branches and capitula erect, seldom pendent; capitula c. 3--5 mm long.

Plants with entire leaves and/or pendent branches are most frequent on the coasts of the Adriatic.

Artemisia caerulescens L. ssp. gallica (Willd.) K. Persson comb. nov.

A. gallica Willdenow 1803 p. 1834. -- A. maritima L. ssp. gallica (Willd.) Burnat 1916 p. 70. -- Original collection: "Gallia" (B, Herb. Willd. no. 15390:4, lectotype).

DISTRIBUTION: Spain (north-eastern coast, Isla Baleares), France (south coast, Corse), Italy (Sardinia).

Flowering shoots c. 15--40 cm. Leaves on lower third of stem pinnatisect with primary segments usually about 3--6 mm long, ultimate segments very short, c. 0.4--0.7 mm broad. Branches and capitula erect; capitula c. 2.5--4 mm long.

Intermediate forms are frequent in the area where the two subspecies meet, i.e. Corse and Sardinia. Thus, plants with very short internodes, dense synflorescences and pinnatisect leaves were described from Corse as A. densiflora by Viviani (1830 p. 4), and very similar plants are also found on the French south coast, especially in the Marseille area. Other plants from the same and other Corsican localities (and Sardinia) are more like "typical" A. caerulescens, with a taller stature, less segmented leaves, etc.

## SPECIATION AND DISTRIBUTION

According to Krashennnikov (1946) there seem to be six principal centres of speciation of Artemisia in Eurasia. These he calls: 1) Chino-nipponese 2) Angarian 3) Beringian 4) Central Asiatic 5) Mid-Asiatic and 6) European-Mediterranean. Within the subgenus Seriphidium the highest concentration of species, 16--20 (Krashennnikov op. cit., Jäger 1971), is found within the area corresponding to Krashennnikov's "Mid-Asiatic" centre, i.e. the area immediately east of the Caspian Sea, and north and south-east of this area are 5--15 species. Very probably this Mid-Asiatic area has had a principal rôle as a centre of differentiation and speciation in Seriphidium. However, the possibility cannot be excluded that some of the taxa in the Artemisia maritima complex may have become differentiated within the European-Mediterranean region, possibly during or even before the Late-glacial.

Most of the species within the A. maritima complex are confined to steppes or similar habitats, and often on saline or calcareous substrates. In such mostly very arid areas the populations often fluctuate in size or are broken up into semi-isolated subunits, a population structure that is most favourable for rapid evolution (Wright 1940). Much of the speciation within the complex has quite possibly been of the type quantum speciation (Grant 1963 pp. 456--459), i.e. the budding off of a new and different daughter species from a semi-isolated peripheral population. Structural differences such as inversions probably played an important part in the differentiation of the new species or subspecies. Particularly if the inversions are short, the genes within the inversions will be effectively linked, as the chances of double crossing-over (prerequisite for recombination within an inversion) are diminished. If the combination of genes within an inversion has a selective value in a given environment, the inversion itself will also have a similar value as a preserver of the gene combination. In A. maritima it was shown that inversions are quite common in the populations and that in local races different types of inversions had probably taken place (p. 91). Such conditions indicate the rôle of inversions in subdividing the species into races (cf. Stebbins 1950 p. 421).

The conditions prevalent in the habitats of the Seriphidia, especially during Glacial and Late-glacial times, were also particularly favourable for hybridization and polyploidization, i.e. the formation of allopolyploids. As was discussed previously, the polyploids



of Seriphidium (and other Artemisiae) are probably of hybridogenic origin. According to Stebbins (1950 pp. 347--348) polyploids are particularly well suited for colonizing newly exposed habitats, e.g. such as formed by the retreat of ice sheets, but Manton (1950) maintains instead it is the climatic and other disturbances that promote hybridization and thus favour the formation and establishment of new allopolyploids.

During the Late-glacial most of the non-glaciated parts of Europe were still devoid of forests. According to van der Hammen et al. (1971) northern Europe during the Late-glacial, and especially between 13,000 and 11,800 B.C., was characterized by a relatively high percentage of steppe elements, such as Artemisia and Chenopodiaceae. Such steppe elements are more frequent in deposits from the Late-glacial than from earlier periods of the last glaciation, as the climate was apparently always much drier during the later parts of a glacial period than at the beginning. The vegetation was probably more of a kind of steppe tundra than a typical steppe owing to the low temperatures. The Mediterranean area also had a steppe period (op. cit.), most pronounced at the beginning of the Late-glacial (14,000 B.C.). The Mediterranean steppes were a westward extension of the cool or cold steppe zone of Central Asia. Apart from being favourable habitats for speciation and hybridization, the steppe and steppe tundra regions in Europe formed excellent migratory routes for the new and old species. There were probably two principal migratory routes from the east, either a Central European one via the Pannonic basin, or a North Mediterranean one south of the Alps. The feasibility of a third possible migratory route via the South Mediterranean is not great as today there are no taxa closely related to the A. maritima complex in North Africa. During the Post-glacial when forest vegetation rapidly migrated to formerly more or less tree-less areas, the distribution areas of the Artemisiae and other steppe species were also rapidly reduced into mostly small areas of a relict nature, such as in central Germany, dry valleys in the Alps, and the Pannonic area, most of which are now covered with an edaphically rather than climatically conditioned steppe vegetation, or else the species were isolated in coastal regions.

The A. lerchiana group is an example of a group with a disjunct distribution, the species nowadays being confined to small areas often of a relict type. Both diploids and tetraploids seem to have

a restricted or disjunct distribution. Thus, A. lerchiana (tetraploid?) is distributed in three different isolated areas, viz., 1) south-eastern European Russia, western Kazakhstan and western Siberia, 2) the Crimea, and 3) some localities in western Roumania and Bulgaria. Particularly in the last-mentioned localities, the substrate is often calcareous (e.g. rock crevices and steppe rudiments). Such a substrate also characterizes the habitats of A. dzevanovskii in its limited area of distribution on the Tarkhankutsk peninsula in the Crimea. A. taurica (diploid and tetraploid?) also has a very disjunct distribution, the largest continuous area being in the Crimea, and smaller areas being localized in the Caucasus and around the lower Don and Volga. This species is more commonly found on saline substrates than the above-mentioned ones are, and, according to Leonova (1970), it also sometimes invades disturbed areas (characteristic for many polyploids, especially fairly newly-formed ones). The only species of this group that appears to have migrated towards Central Europe is A. vallesiaca (tetraploid). This species and others belonging to a Euro-Siberian Stipa capillata steppe (e.g. Koeleria vallesiana) were probably spread during the Late-glacial and Post-glacial via Central European and/or North Mediterranean routes (cf. Bolós 1951). According to Wendelberger (1960) certain valleys in the Alps (e.g. in Valais), which now harbour several species of a relict or disjunct type, e.g. A. vallesiaca, A. atrata and A. borealis, probably served as refuges during the last period of glaciation. Thus, A. vallesiaca may even have immigrated into the present area of distribution before the last glaciation and survived the period in one of the refuges. Under conditions of increasing temperature, a species might advance upwards on the mountains, and with decreasing temperature it might retreat into the valleys, thus even migrating over mountain ranges. This is probably the explanation of the present area of distribution of A. vallesiaca, divided into two smaller areas now totally isolated from each other (the Rhône valley and the Aosta valley). The valleys (and other presumed glacial refuges in the Alps) are now characterized by a very arid climate and vegetation of a steppe-like nature or at least containing many steppe elements. According to Ehrendorfer (1968) stable communities such as those of A. vallesiaca ("Dauergesellschaften") often tend to harbour old relict types, while successional and climax biotopes allow for the expansion of more recent elements. A. vallesiaca is probably a relatively old taxon, judging by not only its distribution but also its very



"stable" morphology and cytology.

The taxa within the morphologically and cytologically variable A. santonicum group are probably younger. For instance, the allopolyploid derivatives within A. santonicum are not yet sufficiently differentiated to be easily distinguishable, although this may also depend on a low rate of differentiation. One of the diploid parents, A. santonicum ssp. patens, now has a very restricted distribution, though formerly this was probably much larger and perhaps comprised much of southern Russia and the Caspian region. The allopolyploids were probably formed either somewhere in the Caspian region before the last period of glaciation or during the period of migration to the Roumanian and Pannonic regions. Faced with competition from the vigorous polyploids, the diploid form then retreated to its present restricted area, an area known to harbour many relicts of a south-eastern flora once more widespread during the warm and dry early Post-glacial but later impoverished as temperatures decreased (Wendelberger 1950). The other diploid involved in the parentage of A. santonicum ssp. santonicum is perhaps extinct, or alternatively it may be one of the Seriphidia of the Caspian area. A. nutans is very like A. santonicum, and it appears to be diploid (though this has not been determined with certainty), so it cannot be disregarded as a possible parent. It has a totally different habitat (confined to cretaceous substrates) as compared with A. santonicum ssp. santonicum, but polyploids have often been found to have a wider or different tolerance to ecologic conditions than their parents. A. pauciflora (diploid) is less likely as a parent of A. santonicum ssp. santonicum, though they have some characters in common, but in the main they are quite different and easily distinguishable.

In contrast to the above-mentioned groups, the A. caerulescens group does not comprise any polyploids, and the diploids are vigorous and have a fairly wide distribution (large parts of the North Mediterranean coasts). Morphological variation is extensive, and there is also some cytological variation, probably due to structural rearrangements (cf. A. caerulescens in Portugal--France versus Yugoslavia). Structural heterozygosity is common. The group probably migrated into its present area of distribution via a route south of the Alps and was perhaps formerly distributed somewhat further to the east but hardly north of the Alps, as A. caerulescens is obviously a species adapted to much warmer conditions than the previously mentioned groups (on the Atlantic coast it does not

advance further north than half-way up the coast of Portugal). It is quite possible that A. caerulescens was even differentiated as a species within the Mediterranean region. Some racial differentiation has also taken place within the species. Thus, there is one ecotype in Romagna (Italy) confined to inland localities on calcareous substrates (var. cretacea Fiori).

As for the origin of hexaploid A. maritima, the species is nowadays so well differentiated morphologically and geographically isolated that to speculate on its presumed parentage is difficult. The species is obviously of hybridogenic origin (allopolyploid), which was earlier suggested by Gams (1928), who presumed that A. vallesiaca, A. pauciflora and A. caerulescens were involved in the parentage. The present author agrees that one of the A. lerchiana group (A. vallesiaca?) might well be involved in the origin of A. maritima, and perhaps also A. caerulescens, but it is only a guess based on the general appearance of these species. As with many other Artemisia species, A. maritima was probably widespread in Europe during the Late-glacial. When the ice sheets retreated and forests invaded the former steppes, the species became isolated in relict localities (central Germany) and coastal areas. Differentiation into two subspecies probably took place before the Swedish Late-glacial. Ssp. humifusa perhaps evolved on more calcareous substrates, typical for many areas during the last glaciation before the till became leached. When the ice sheet and the waters of the Baltic had retreated from the Baltic islands, and probably just before the Ancylus transgression, when the sea-level was extremely low (8000--7500 B.C.), a considerable part of the Öland--Gotland flora invaded the area (Terasmäe 1951), possibly also A. maritima ssp. humifusa. Its present distribution is probably of a relict nature, as is the case with many other species, mostly steppe elements, of the flora on Öland, Gotland and Saaremaa, e.g. Artemisia rupestris, A. oelandica, Ranunculus illyricus and Plantago tenuiflora. Many of these species have a distribution corresponding almost exactly to that of A. maritima and/or other Seriphidia. Thus the species most closely related to hexaploid Artemisia oelandica (and once considered as conspecific), A. laciniata, is distributed in the Pannonic area and in Russia and has only recently died out in the Artern area (central Germany). A. rupestris is distributed on Öland, Gotland and the islands outside Estland, in the Artern area and in Russia, Plantago tenuiflora on Öland, in the Pannonic area and in Russia. The above-mentioned species often grow on somewhat saline substrates, though not in the Baltic area,



contrary to A. maritima ssp. humifusa. Brugg-Schlegel (1963) also emphasized the relationship between the vegetation on limestone on Öland--Gotland and the Middle European vegetation on dry soils (e.g. in Valais, cf. A. vallesiaca). Thus, he even referred some calcicolous vegetation on Öland--Gotland to communities within "Festucetalia vallesiaceae". For instance, Ephedra, a genus represented in the Artemisietum vallesiaceae, was growing on Öland as late as Post-glacial times (Iversen 1954).

During the whole of the Late-glacial a steppe vegetation comprising species such as Ephedra, Chenopodiaceae, Artemisia maritima (ssp. humifusa?) and other Seriphidia still existed near Leningrad (Gričuk 1951), but all steppe elements later disappeared, and forest vegetation had invaded the area at the beginning of the Boreal (7000--6500 B.C.). This was apparently the time when A. maritima ssp. humifusa became isolated in its present area of distribution, like many other steppe relicts in this area.

A. maritima ssp. maritima may have invaded Scandinavia somewhat later than ssp. humifusa but before the land-bridge Germany--Denmark--Sweden was broken. A. maritima thus seems to have migrated into Scandinavia along different routes and perhaps at different times. The diploids Galium oelandicum and G. suecicum of the G. pumilum complex (Ehrendorfer 1962) constitute a similar case of two closely related taxa with different immigration history. Thus, G. oelandicum is presumed to have migrated to Öland during the regression of the Yoldia Sea, and G. suecicum invaded Scandinavia only later, after the Preboreal.

When the forest invaded the former steppes, A. maritima ssp. maritima became isolated in a restricted area in central Germany and on the coasts of north-western Europe. The competitive capacity of the subspecies is probably as low as in many other Artemisia species, not only as seen by the type of distribution in itself, but also because the subspecies is now close to extinction in the Artern area, as is the case with A. rupestris and A. laciniata (probably already extinct), and it is even on the retreat in many coastal areas, particularly in France, Great Britain and parts of Scandinavia. The only area in which A. maritima ssp. maritima is still expanding seems to be the archipelagos of Bohuslän (Sweden), according to Sjöström (1968) and others (personal communication). This is an interesting observation as the populations in Bohuslän constitute a special ecotype within ssp. maritima as yet not suf-

ficiently morphologically differentiated to be classified as a separate subspecies.

The evolutionary situation within the Artemisia maritima complex in Europe may be summarized as follows:

1) Polyploids dominate somewhat over diploids within the complex both in number of taxa and in area of distribution.

2) One group within the complex consists of diploids only with a fairly wide distribution and a high degree of variability, and is obviously in the course of initial differentiation with some races already sufficiently distinct to be taxonomically classified as subspecies or varieties (the A. caerulescens group).

3) In another group the diploids have a restricted distribution but are still characterized by a high degree of variability; the diploid/polyploid populations seem to be in the course of initial differentiation and are not yet sufficiently distinct to be classified as taxonomic species (the A. santonicum group).

4) In a third group polyploids (and diploids?) are split up into disjunct areas of a relict nature consisting of stable communities, and the species are both morphologically and cytologically distinct and characterized by a moderate degree of variability (the A. lerschiana group).

5) The fourth group comprises high-polyploids only, which are extremely variable both morphologically and cytologically but sufficiently divergent from the rest of the complex to make the question of their origin a highly speculative one; the group is still in the course of differentiation and comprises both old and new ecotypes, but it is apparently already on the decline after a period of expansion, and is now retreating in many localities (the A. maritima group).





## LITERATURE CITED

- Allioni, C. 1774. Auctuarium ad Synopsim Methodicam Stirpium Horti Regi Taurinensis. -- Mélang. Philos. Math. Soc. Roy. Turin 5:53--96.
- Anderson, E. 1936. An experimental study of hybridization in the genus *Apocynum*. -- Ann. Missouri Bot. Gard. 23:159--167.
- Arano, H. 1962. Cytological studies in subfam. Carduoideae of Japanese Compositae. VI. Karyotype analysis in the genus *Artemisia*. -- Bot. Mag. (Tokyo) 75:356--368.
- 1963. Cytological studies in subfamily Carduoideae (Compositae) of Japan. XIV. The karyotype analysis in genus *Artemisia* (3). -- Bot. Mag. (Tokyo) 76:459--465.
- 1964. Cytotaxonomic studies in subfam. Carduoideae of Japanese Compositae. XI. The karyotype analysis in some species of *Artemisia*. -- Kromosomo 59:1883--1888.
- Arnold, A. 1955. Die Bedeutung der Chlorionen für die Pflanze. -- Bot. Stud. 2. Jena.
- Bartholomew, J. (ed.) 1955. The Times atlas of the world, 3. Northern Europe. -- London.
- 1956. Ibid., 4. Southern Europe and Africa. -- London.
- Beguinot, A. 1908. Sul prevalente sviluppo omoblastico in alcune alofite. -- Bull. Soc. Bot. Ital. Firenze 1908:29--30.
- Bentzer, B. 1969. Chromosome morphology in Aegean populations of *Leopoldia* Parl. (Liliaceae). -- Bot. Notiser 122:457--480.
- 1972. Variation in the chromosome complement of *Leopoldia comosa* (L.) Parl. (Liliaceae) in the Aegean (Greece). -- Ibid. 125:406--418.
- , Bothmer, R. von & Wendelbo, P. 1972. Chromosome morphology in Afghanian *Bellevalias* (Liliaceae). -- Ibid. 125:153--156.
- Berg, C. C. 1967. Cytotaxonomic studies in *Cardamine pratensis* L. in The Netherlands. -- Acta Bot. Neerl. 15:683--689.
- Besser, W. S. J. G. von. 1829. Synopsis Absynthiorum. -- Bull. Soc. Nat. Mosc. 1.
- 1834. De Seriphidiis. -- Ibid. 7:5--46.
- 1835. De Dracunculis. -- Ibid. 8:1--97.
- Blakeslee, A. F. 1930. Extra chromosomes, a source of variation in the Jimson weed. -- Smithsonian Report 1930:431--450.
- Bolós, O. de. 1951. Algunas consideraciones sobre las especies esteparias en la Peninsula Ibérica. -- Anal. Jard. Bot. Madrid 10:1--9.
- Bonner, J. & Galston, A. W. 1958. Principles of plant physiology. -- San Francisco.



- Brandham, P. E. 1969. Chromosome behaviour in the Aloineae. I. The nature and significance of E-type bridges. -- *Chromosoma* (Berlin) 27:201--215.
- Braun-Blanquet, J. 1963. Das Helianthemo-Globularion, ein neuer Verband der baltischen Steppenvegetation. -- *Station Intern. Géobot. Médit. et Alp., Comm.* (Montpellier) 160.
- Burnat, E. 1916. Flore des Alpes Maritimes, 6 (1). -- Genève, Bâle & Lyon.
- Cassini, A. H. G. Comte de. 1817. Aperçu des genres ou sousgenres nouveaux formés par..... dans la famille des Synantherées. -- *Bull. Sci. Soc. Philom. Paris* 1817:33.
- Chapman, V. J. 1942. The new perspective in the halophytes. -- *Quart. Rev. Biol.* 17 (4):291--311.
- 1960. Salt marshes and salt deserts of the world. -- London, New York.
- Chiovenda, E. 1912. Della priorità di alcuni nomi specifici di piante contenuti nell "Auctuarium ad Synopsim Methodicam Stirpium Horti Regi Taurinensis" dell' Allioni pubblicato nel 1774. -- *Ann. Bot.* 10:15--23.
- Clapham, A. R., Tutin, T. G. & Warburg, E. F. 1962. Flora of the British Isles, ed. 2. -- Cambridge.
- Cleland, R. E. 1949. Phylogenetic relationships in Oenothera. -- *Proc. 8th Intern. Congr. Genetics* (Hereditas Suppl. vol.):173--188.
- Colwell, R. N. 1951. The use of radioactive isotopes in determining spore distribution patterns. -- *Amer. Journ. Bot.* 38:511--523.
- Darlington, C. D. 1932. Recent advances in cytology. -- London.
- & La Cour, L. F. 1950. Heredity selection in Campanula. -- *Heredity* 4:217--248.
- Delf, E. M. 1911. Transpiration and behaviour of stomata in halophytes. -- *Ann. Bot.* 25:485--505.
- Diettert, R. A. 1938. The morphology of *Artemisia tridentata* Nutt. -- *Lloydia* 1:3--74.
- Duncan, R. E. 1945. Production of variable aneuploid numbers of chromosomes within the root tips of *Paphiopedilum wardii* Summerhayes. -- *Amer. Journ. Bot.* 32:506--509.
- Eames, A. J. 1961. Morphology of the Angiosperms. -- New York, Toronto & London.
- Ehrendorfer, F. 1953. Systematische und zytogenetische Untersuchungen an europäischen Rassen des *Achillea millefolium*-Komplexes. -- *Österr. Bot. Zeitschr.* 100:583--592.
- 1959 a. Spontane Chromosomenaberrationen und andere Meiosestö-

- rungen bei diploiden Sippen des *Achillea millefolium*-Komplexes. Zur Phylogenie der Gattung *Achillea*, II. -- *Chromosoma* (Berlin) 10:365--406.
- 1959 b. Differentiation-hybridization cycles and polyploidy in *Achillea*. -- Cold Spring Harbour Symp. Quant. Biol. 24:141--152.
- 1962. Cytotaxonomische Beiträge zur Genese der mitteleuropäischen Flora und Vegetation. -- *Ber. Deutsche Bot. Ges.* 75:137--152.
- 1964. Notizen zur Cytotaxonomie und Evolution der Gattung *Artemisia*. -- *Österr. Bot. Zeitschr.* 111:84--142.
- 1968. Geographical and ecological aspects of infraspecific differentiation. -- In V. H. Heywood (ed.): *Modern methods in plant taxonomy*, pp. 261--296. -- London.
- Eijk, M. van. 1939. Analyse der Wirkung des NaCl auf die Entwicklung, Sukkulenz und Transpiration bei *Salicornia herbacea*, sowie Untersuchungen über den Einfluss der Salzaufnahme auf die Wurzelatmung bei *Aster tripolium*. -- *Rec. Trav. Bot. Neerl.* 36:559--657.
- Ferri, S. 1964. *Artemisia caerulescens* L. var. *cretacea* Fiori: indagine morfologica, anatomica ed analitica. -- *Giorn. Bot. Ital.* 71:68--95.
- Fries, E. M. 1845. *Summa Vegetabilium Scandinaviae*. -- Upsaliae.
- Fritsch, V. *Schedae ad Floram exsiccatam Austro-Hungaricam* no. 2265. -- 1897. *Excursionsflora für Österreich*. -- Wien.
- 1909. *Ibid.*, ed. 2. -- Wien.
- Fuchs, H. P. 1960. *Saxifraga crustata* oder *Saxifraga incrustata*? -- *Phyton* 9 (1, 2):42.
- Gadella, T. W. J. & Kliphuis, E. 1968. Chromosome numbers of flowering plants in the Netherlands, IV. -- *Meded. Bot. Mus. Herb. Rijksuniv. Utrecht* 274:168--183.
- Gams, H. 1928. *Artemisia*. -- In G. Hegi: *Illustrierte Flora von Mitteleuropa*, 6 (2), pp. 626--672. -- München.
- Gillner, V. 1965. Salt marsh vegetation in southern Sweden. -- In *The plant cover of Sweden*. -- *Acta Phytogeogr. Suec.* 50:96--104.
- Good, R. 1964. *The geography of the flowering plants*, ed. 3. -- London & Colchester.
- Gorenflot, R. 1968. Chromosomes surnuméraires et mosaïques chromosomiques chez *Plantago coronopus* L. -- *Compt. Rend. Soc. Biol.* 162: 17--21.
- Grant, V. 1963. *The origin of adaptations*. -- New York & London.
- 1967. Linkage between morphology and viability in plant species. -- *Amer. Nat.* 101:125--139.
- 1971. *Plant speciation*. -- New York & London.
- Gray, A. 1884. *Synoptical flora of North America*, 1 (2). -- New York.



- Grenier, J. C. M. & Godron, D. A. 1850. Flore de France, ou Description des plantes qui croissent naturellement en France et en Corse, 2 (1). -- Paris.
- Gričuk, V. P. 1951. Über die trockene Periode des Postglazials im Europäischen Teil der UdSSR. -- Voprosy Geografii 24:165--191.
- Håkansson, A. 1950. Spontaneous chromosome variation in the roots of a species hybrid. -- Hereditas 36:39--59.
- Hall, H. M. & Clements, F. E. 1923. The phylogenetic method in taxonomy. The North American species of *Artemisia*, *Chrysothamnus* and *Atriplex*. -- Carnegie Inst. Washington Publ. 326:1--355.
- Hammen, T. van der, Wijmstra, T. A. & Zagwijn, W. H. 1971. The floral record of the late Cenozoic of Europe. -- In K. K. Turekian (ed.): The late Cenozoic glacial ages, pp. 391--424. -- New Haven & London.
- Harling, G. 1950. Embryological studies in the Compositae. -- Acta Horti Berg. 15 (9):135--168.
- Hartman, C. J. 1820. Handbok i Skandnaviens flora. -- Stockholm.
- 1879. Ibid., ed. 11. -- Stockholm.
- Heneen, W. K. & Runemark, H. 1962. Chromosomal polymorphism and morphological diversity in *Elymus rechingeri*. -- Hereditas 48:545--564.
- Hess, H. E., Landolt, E. & Hirzel, R. 1972. Flora der Schweiz, 3. -- Basel.
- Hultén, E. 1950. Atlas över växternas utbredning i Norden. -- Stockholm.
- Iversen, J. 1954. The Late-glacial flora of Denmark and its relation to climate and soil. -- Danmarks Geol. Unders., 2. Raekke, 80.
- Jacquet, J. 1949. Recherches écologiques sur le littoral de la Manche. -- Encycl. Biol. Ecol. 5. -- Paris.
- Jäger, E. J. 1971. Die pflanzengeographische Stellung der "Steppen" der Iberischen Halbinsel. -- Flora (Jena) 160:217--256.
- John, B. & Lewis, K. R. 1965. The meiotic system. -- Protoplasmatologia. -- New York.
- Jonsell, B. 1968. Studies in the North-west European species of *Rorippa* s. str. -- Symb. Bot. Upsal. 19 (2).
- Kawatani, T. 1950. (In Japanese, no English summary). -- Agriculture and Horticulture (Japan) 25:1004.
- 1952. On the scientific name of "Mibuyomogi", the santonin source in Japan. -- Journ. Pharm. Soc. Jap. 72:721--722.
- & Ohno, T. 1960. On the santonin content in Thuringian wild *Artemisia maritima* L. cultivated at Kasukabe. -- Bull. Nat. Inst. Hyg. Sci. 78:49--53.
- & -- 1964. Chromosome numbers in *Artemisia*. -- Ibid. 82:183--193.
- Keck, D. D. 1946. A revision of the *Artemisia vulgaris* complex in

- North America. -- Proc. Calif. Acad. Sci. 4th Ser. 25:421--468.
- Khoshoq, T. N. & Sobti, S. N. 1958. Cytology of Indian species of *Artemisia*. -- Nature 181:853--854.
- Kitamura, S. 1957. Compositae Japonicae, pars sexta. -- Mem. Coll. Sci. Kyoto Univ., Ser. B, 24 (1):1--79.
- Klokov, M. V. 1962. *Artemisia* -- In E. D. Vissyulina (ed.): Flora URSS, 11. -- Kijiv.
- Koch, W. D. J. 1837. Synopsis Florae germanicae et helveticae. -- Francofurti a. M.
- Koul, M. L. H. 1964. Cytomorphological survey of Indian *Artemisia* L. -- Journ. Sci. Res. Banaras Hindu Univ. 14 (2):103--110.
- Krashennnikov, I. M. 1946. Opyt filogenetičeskogo analiza nekotorykh evraziatskikh grupp roda *Artemisia* L. svyazi s osobennostyami paleogeografii Evrazii. -- Mat. po Ist. Flor. i Rast. SSSR 2:87--196.
- Lamarck, J. B. A. P. de. 1783. Encyclopédie Méthodique. Botanique, 1. -- Paris.
- & DeCandolle, A. P. 1805. Flore française, ed. 3, 4. -- Paris.
- Lanjouw, J. & Stafleu, F. A. 1964. Index Herbariorum, 1. -- Regn. Veg. 31.
- Lawrence, G. H. M. 1951. Taxonomy of vascular plants. -- New York.
- Ledebour, C. F. von. 1845. Flora rossica, 2 (2). -- Stuttgartiae.
- Lellep, E. 1958. Meripuju (*Artemisia maritima* L. s. l.) levikust tema areaali põhjapiiril. -- Tartu Riik. Ülik. Toim. 64:154--167.
- Leonova, T. G. 1969. *Artemisia* -- In E. V. Wulf: Flora Kryma, 3 (3), pp. 210--223, 360--364. -- Jalta.
- 1970. Notulae criticae de subgenere *Seriphidium* (Bess.) Rouy generis *Artemisia* L. florum partis europaeae URSS. -- Nov. Syst. Pl. Vasc. (Leningrad) 7:280--294.
- Lewis, W. H. 1962. Aneusomaty in aneuploid populations of *Claytonia virginica*. -- Amer. Journ. Bot. 49:918--928.
- 1967. Cytocatalytic evolution in plants. -- Bot. Rev. 33:105--115.
- Lewis, K. R. & John, B. 1966. The meiotic consequences of spontaneous chromosome breakage. -- Chromosoma 18:287--304.
- Liljeblad, S. 1816. Utkast till en svensk flora, ed. 3. -- Upsala.
- Linnaeus, C. 1753. Species plantarum. -- Holmiae.
- Löve, A. 1964 a. The evolutionary framework of the biological species concept. -- Genetics today (Proc. 11th Int. Congr. Genet.), pp. 409--415. -- The Hague.
- 1964 b. The biological species concept and its evolutionary structure. -- Taxon 13:33--45.
- Manton, I. 1950. Problems of cytology and evolution in the Pteridophyta. -- Cambridge.



- Magumori, S. 1961. Cytological studies on *Artemisia*. I. Karyotypes of five diploid species. -- Bull. Fac. Education, Yamaguchi Univ., 9 (2):43--56.
- Meyer, M. 1965. Beiträge zur Aneusomatie dargestellt an *Begonia x tuberhybrida* und einige Wildarten. -- Biol. Zentralbl. 84:563--605.
- Milhofer, J. 1933. Botanische und chemische Untersuchungen an *Artemisia caerulescens* L. -- Acta Bot. Inst. Bot. Univ. Zagreb 8:1--96.
- Mitsuoka, S. 1961. Cytogenetical studies on  $F_1$  hybrids between *Artemisia maritima* L. ssp. *monogyna* Waldst. & Kit. and *A. lercheana* Stech. var. *dahurica* Kitam. -- Seiken Zihô (Rep. Kihara Inst. Biol. Res.) 12:70--74.
- Montfort, C. 1927. Über Halobiose und ihre Abstufung: Versuch einer synthetischen Verknüpfung isolierter analytischer Problem. -- Flora 21:433--502.
- & Brandrup, W. 1927. Physiologische und pflanzengeographische Seesalzwirkungen. 2. Ökologische Studien über Keimung und erste Entwicklung bei Halophyten. -- Jahrb. Wiss. Bot. 66:902--946.
- & -- 1928. Physiologische und pflanzengeographische Seesalzwirkungen. 3. Vergleichende Untersuchung der Salzwachstumsreaktionen von Wurzeln. -- Ibid. 67:105--173.
- Müntzing, A. 1930. Outlines to a genetic monograph of *Galeopsis*. -- Hereditas 13:185--341.
- 1945. On the causes of inbreeding degeneration. -- Arch. Julius Klaus-Stift., Ergänzungsband zu Band 20:153--163.
- & Prakken, R. 1940. The mode of chromosome pairing in *Phleum* twins with 63 chromosomes and its cytogenetic consequences. -- Hereditas 26:463--501.
- Neilreich, A. 1859. Flora von Nieder-Österreich. -- Wien.
- Östergren, G. & Heneen, W. K. 1962. A squash technique for chromosome morphological studies. -- Hereditas 48:332--341.
- Patterson, B. 1965. Gotland and Öland, two limestone islands compared. -- In The plant cover of Sweden. -- Acta Phytogeogr. Suec. 50:131--140.
- Poljakov, P. P. 1961. *Artemisia* -- In V. L. Komarov et al.: Flora SSSR, XXVI, pp. 425--631. -- Moskva & Leningrad.
- Pólya, L. 1947. Szíki növények kromoszómaszámai. -- Diss. Debrecen.
- 1948. Chromosome numbers of certain alkali plants. -- Arch. Biol. Hung. 2 (18):145--148.
- Poma, G. 1922. L'Influence de la salinité de l'eau sur la germination et la croissance des plantes halophytes. -- Acad. Roy. Belg. Bull. Class. Sci., Ser. 5, 8 (2):81.

- Pragłowski, J. 1971. The pollen morphology of the Scandinavian species of *Artemisia* L. -- *Pollen et Spores* (Paris) 13 (3):381--404.
- Rees, H. 1961. Genotypic control of chromosome form and behaviour. -- *Bot. Rev.* 27:288--318.
- Reese, G. 1954. Euploidie, Aneuploidie und B-Chromosomen bei *Caltha palustris* L. -- *Planta* 44:203--268.
- Reichenbach, L. 1830--1832. *Flora Germanica Excursoria*, 1--2. -- *Lipsiae*.
- Rouy, G. C. C. 1903. *Flore de France*, 8. -- Asnières, Paris & Rochefort.
- Rychlewski, J. 1967. Karyological studies on *Nardus stricta* L. -- *Acta Biol. Cracov., Ser. Bot.*, 10:55--72.
- Rydberg, A. 1916. *North American Flora*, 34 (3). -- New York.
- Sagorski, E. 1907. Über *Artemisia salina* Willd. erweitert. -- *Österr. Bot. Zeitschr.* 57:14--18.
- 1908. Die Formen der *Artemisia salina* Willd. am Soolgraben bei Artern nebst einigen ungarischen Formen. -- *Mitt. Thür. Bot. Ver.* 23:61--90.
- Salisbury, R. A. 1796. *Prodromus Stirpium in Horto ad Chapel Allerton vigentium*. -- Londini.
- Seratz, E. 1937. Beiträge zur Biologie der Halophyten. 4. -- *Jahrb. Wiss. Bot.* 84:593--638.
- Schub, P. J. F. 1853. *Sertum Florae Transsilvaniae*. -- *Verh. Siebenb. Ver. Naturw.* 4.
- 1860. Zur Flora von Siebenbürgen. Berichtigungen und Nachträge. 2. -- *Österr. Bot. Zeitschr.* 10:227--229.
- Sears, E. R. 1944. Cytogenetic studies with polyploid species of wheat. II. Additional chromosomal aberrations in *Triticum vulgare*. -- *Genetics* 29:232--246.
- 1954. The aneuploids of common wheat. -- *Univ. Missouri Res. Bull.* 572:1--58.
- Sharma, A. K. 1956. A new concept of a means of speciation in plants. -- *Caryologia* 9:93--130.
- & Bhattacharyya, U. C. 1957. Cytological studies in *Begonia*. I. -- *La Cellule* 58:307--329.
- Shimotomai, N. 1947. The polyploidy in the genus *Artemisia*. -- *Jap. Journ. Genet.* 22:29--30.
- , Adachi, S. & Masumori, S. 1968. Cytological, morphological and geographical studies on *Chrysanthemum shiwogiku* var. *kinokuniense*. -- *Bot. Mag. (Tokyo)* 81:498--505.
- Singh, G. & Joshi, R. D. 1969. Pollen morphology of some Eurasian



- species of *Artemisia*. -- Grana palynol. 9:50--62.
- Stebbins, G. 1935. Somatic instability of chromosome number in *Hymenocallis calathinum*. -- Heredity 9:129--134.
- Stebbins, G. 1937. Taxonomic literature. -- Utrecht.
- Stebbins, G. 1938. Cytogenetic studies in *Paeonia*. II. The cytology of the diploid species and hybrids. -- Genetics 23:83--110.
- 1947. Types of polyploids: their classification and significance. -- Advances in Genetics 1:403--429.
- 1950. Variation and evolution in plants. -- New York.
- Stroobant, J. P. 1775. Dissertatio inauguralis Botanico Medico de *Artemisia*. -- Goettingae.
- Ström, E. 1952. Zur Feinmorphologie des Pollens von *Salix* und von *Artemisia*. -- Sv. Bot. Tidskr. 46:204--227.
- Sundström, S. 1956. Vegetation och flora i Skaftö socken i mellersta Bohuslän. -- Sv. Bot. Tidskr. 62:1--120.
- Suzuki, O. 1949. Chromosome numbers in *Artemisia*. -- Abstr. 21st Ann. Meet. Genet. Soc. Japan 1949:1--3.
- 1950. Chromosome numbers in the genus *Artemisia*. -- Jap. Journ. Genet. 25 (1):17--18.
- 1952. Chromosome numbers in *Artemisia*. I. -- Seiken Zihô (Rep. Kihara Inst. Biol. Res.) 5:68--77.
- & Kurihara, S. 1949. Chromosome numbers of medical plants. I. -- Jap. Journ. Pharmacogn. 3:68--74.
- Sussman, G. P. 1955. Cytology and cytogenetics. -- London.
- Tarcea, I. I. 1948. Die Chromosomenzahlen der Anthophyten-Flora von Rumänien mit einem Ausblick auf das Polyploidie-Problem. -- Bul. Grădin. Bot. Mus. Bot. Univ. Cluj 28, Suppl.:1--130.
- Taylor, M. 1939. Salt tolerance of Long Island salt marsh plants. -- Circ. N. Y. State Mus. 23:1--42.
- Terasaki, H. & Mikiyama, U. 1939. Some considerations on the classification of *Crya sativa* L. into two subspecies, so-called "japonica" and "indica". -- Jap. Journ. Bot. 10:213--258.
- Terasaki, U. 1951. Identification of pollen grains and spores in Late-glacial deposits from Gotland, Sweden. -- Sv. Bot. Tidskr. 45: 501--515.
- Tikhon, N. N. 1935. Poiski rastelnoj drozofily. -- Sov. Bot. 2:61--67.
- Tillett, W. G. 1946. *Suaeda novae-zelandiae* (Allan sp. nov.). An autoecological study. -- M. Sc. thesis, Auckland Univ.
- Uphof, J. C. T. 1941. Halophytes. -- Bot. Rev. 7:1--58.
- Vanderhaeghe, A. 1949. Spindle abnormalities and variation in chromosome number in *Ribes nigrum*. -- Hereditas 35:136--162.

- Vallin, H. 1936. För Hallands Väderö ej förut publicerade fanerogamer och kärlkryptogamer samt i övrigt några för ön intressanta växter. -- Bot. Notiser 1936:519.
- Viviani, D. 1830. Florae Corsicae Specierum novarum vel minus cognitarum Diagnosis quam in Florae italicae Fragmenti alterius Prodromum exhibet. App. 2. -- Genuae.
- Waldstein-Wartenberg, F. A. von & Kitaibel, P. 1799--1802. Descriptiones et Icones Plantarum rariorum Hungariae, 1. -- Viennae.
- Wallroth, K. F. W. 1822. Schedulae criticae de plantis florae Halensis selectis. -- Halae.
- Ward, G. H. 1953. Artemisia, section Seriphidium in North America. -- Contrib. Dudley Herb. 4 (6):155--205.
- Weinack, G. 1971. Variation and taxonomy of Hierochloë (Gramineae) in the Northern Hemisphere. -- Bot. Notiser 124:129--175.
- Weineland-Lieber, F. 1928. Zytologische Untersuchungen an Artemisia-Arten. -- Jahrb. Wiss. Bot. 69:636--686.
- Wendelberger, G. 1950. Zur Soziologie der kontinentalen Halophyten-Vegetation Mitteleuropas. -- Österr. Akad. Mat.-Nat. Klasse 108 (5):1--180.
- 1960. Die Sektionen Heterophyllae der Gattung Artemisia. -- Biblioth. Bot. 125:1--193.
- Willdengw, C. L. 1803. Caroli a Linné Species Plantarum 3 (3), ed. 4 -- Berolini.
- Wright, S. 1940. Breeding structure of populations in relation to speciation. -- Amer. Natural. 74:232--248.
- Yurtsev, B. A. & Zhukova, P. G. 1968. Polyploid series and the taxonomy (on the basis of the analysis of some groups of arctic legumes). -- Bot. Zhurn. 53:1531--1542.



## APPENDIX

## LOCALITIES OF CULTIVATED MATERIAL

Collections by the author unless otherwise stated. Collection numbers within parentheses.

Artemisia maritima L. ssp. maritima, 2n=54 (50--56)

SWEDEN. Bohuslän. Lyse, Trälebergskile, inner part of the bay (45, 90). -- Marstrand, Marstrandsön, Skallen c. 300 m S (46). -- Öckerö: Hyppeln, south-west coast (169); Hönön, north-west coast, Röd c. 1500 m W (49); Öckerön, near the northern point (48, 89); Rörön, Apelvik (170). -- Skaftö, Sörhålet N (171). -- Styrsö: Styrsön, southern point (50); Styrsön, near the southern point, c. 800 m from coll. no. 50 (51, 52); Tistlarne (172); Vinga, small bay on the east shore (53). -- Tjärnö, Nordkoster, Valnäsbukten (47). -- Halland. Landa, Frillesås c. 2000 m N, Lannabukten (35). -- Morup, Morups tänge (10). -- Tvååker, Galtabäck, the harbour (54, 91). -- Varberg, along the road to Getterön (55). -- Värö, Bua (34). -- Skåne. Brunnby, Lerhamn, south of the village (42). -- Bunkeflo: Sigfridsborg (15); Stenören (40); Strandhem (12). -- Eskilstorp, Eskilsdal c. 1500 m WSW (17). -- Gässie, Grönahill c. 1200 m W (16). -- Löddeköpinge, Vikhög c. 1500 m N, Saltviken (13). -- Malmö: Industrihamnen (41); Limhamn, "Ön" c. 500 m S (38); Sibbarp (37); Between Sibbarp and Stenören (39). -- Skanör: North of the church (21); Ljunghusen, north of the station (20). -- Stora Hammar, Näset, Lilla Hammar c. 2000 m NNW (19). -- Tofta, Häljarp (22). -- Torekov, Torekov c. 700 m S (101). -- Tygelsjö, Sjötorp c. 1000 m NW (14). -- Västra Klagstorp, Klagshamn, the factory c. 500 m NNW (11). -- Vellinge, Olsborg c. 500 m W (18).

DENMARK. Ålborg. Egense c. 3000 m S, Klattrup (59). -- Frederiksborg. Graese c. 2000 m W (28). -- Kregme c. 2000 m WNW, Lille Kregme (29). -- Haderslev. Halk c. 3500 m NE, Flovt Strand (61). -- Hjørring. Jerup c. 1000 m ENE, along ditches to the sea (56). -- Jerup c. 1100 m ENE (57). -- Lyngså c. 2500 m SE (58). -- København. Amager, Dragør (23). -- Avedøre Strand (24). -- Gundsømagle c. 2000 m WSW, Vigen (27). -- Vallensbækstrand (25). -- Veddelev, north of the village (26). -- Odense. Agernæs (174). -- Randers. Södring c. 1500 m SSW,

Vasehuse (60). -- Ribe. Ho, c. 1000 m SW of the church (62). -- Store Darum c. 1500 m W (31). -- Tjaereborg c. 2000 m SW (33). -- Tjaereborg c. 2000 m WSW (32). -- Tönder. Emmerlev, c. 1000 m north of the Højer canal (65). -- Hviding c. 2000 m NW (30). -- Römö, c. 200 m north of the road to the mainland (64). -- Römödaemningen, c. 3000 m from the mainland (63). -- Vejle. Hejlsminde (173).

GERMANY. Niedersachsen. Butjadingen, Langwarden c. 1500 m NW (72). -- Ostfriesische Inseln: Juist, the shore below and west of the village (79); Langeoog, c. 200 m east of the village (77); Wangerooge, west of the village (76). -- Ostfriesland: Minsen c. 2000 m NW (74); Voslapp c. 1500 m N (73); Westeraccumersiel c. 2000 m NW (75); Westermarsch c. 2000 m WSW (78). -- Sachsen-Anhalt. Artern, Solgraben, saline spring (124 H. Runemark, 161 BG Halle). -- Schleswig-Holstein. Angeln, Kappeln c. 2000 m NNE, near Rabel (164 B. Nilsson). -- Dithmarschen, Wesselburenerkoog c. 3000 m NW (71). -- Nordfriesische Inseln: Amrum, Wittdün (67); Föhr, Oldsum c. 2000 m NNE (121); Nordstrand, Norderhafen c. 3000 m NE, Elisabeth-Sophien-Koog (118); Nordstrand, Süderhafen (69); Nordstrandischmoor, Neuwarft SE (119); Pellworm, Ostersiel (120). -- Nordfriesland: Husum c. 5000 m NW, Schobüll (70); Klanxbüll c. 5000 m SW, Friedrich-Wilhelm-Lübke-Koog (66); Ockholm c. 2000 m W (68). -- Nordholstein: Fehmarnsundbrücke c. 1000 m S (165 B. Nilsson); Heiligenhafen c. 1000 m ENE (122).

THE NETHERLANDS. Friesland. Ameland, Nes, below the village (81). -- Minnertsga c. 4000 m NW, Firdgum c. 3000 m NNW (82). -- Wierum (80). -- Groningen. Hornhuizen c. 4000 m WNW (84). -- Oostende c. 4000 m NE, Oudeschip (85). -- Noord Holland. Texel, De Cocksdorp (83). -- Zeeland. Zeeuws-Vlaanderen, Terneuzen (175).

FRANCE. Calvados. Cabourg, the mouth of the Dives R. (129). -- Charente-Maritime. La Rochelle c. 4000 m N, Pointe du Plomb (133). -- Somme. St. Valéry-sur-Somme c. 4000 m NW, Le Hourdel (127). -- St. Valéry-sur-Somme c. 800 m WNW, Mollières (128). -- Vendée. Beauvoir-sur-Mer c. 2000 m NW, Epoids (130). -- L'Ile d'Olonne c. 2400 m NNW, La Salaire (131). -- Les Sables d'Olonne c. 3000 m NNW, La Girvière (132).

GREAT BRITAIN. Essex. Canvey Island, Canvey-on-Sea c. 1500 m N (152). -- Mersea Island, near the bridge to the mainland (153). -- Norfolk. Cley c. 2000 m E, Salthouse (154). -- Hunstanton c. 2000 m NE, Thornham (156). -- Wells c. 1500 m NE (155). -- Somerset. Burnham-on-Sea (151). -- Uphill (150).



Artemisia maritima L. ssp. humifusa (Hartm.) K. Pers., 2n=54 (50--56)

SWEDEN. Gotland. Boge, Bogevik, southern part, near the mouth (169). -- Burs, Herte c. 300 m WNW (87). -- Fide, Fidenäs (86). -- Gothem, Botvaldevik, Tummungs c. 500 m NW (8). -- Grötlingbo, Grötlingboudé, inner part of the bay Gansviken (6). -- Lärbro, Stora Hammars, Vägumeviken (9). -- Öja, Burgsvik (5, 36). -- Rone, Ronehamn, north of the harbour (7). -- Sanda, Klintehamn c. 1000 m NNW (88). -- Silte, Kvarnåkershamn (4). -- Öland. Alböke, Karse c. 900 m NE, Stora fjärden (3). -- Böda, Lilla Grundet, Grankullaviken (167 E. Nilsson). -- Bredsätra, Nedre Sandby c. 1200 m ESE (2). -- Persnäs, Östra Södvik, north-eastern corner of the bay Södviken (1).

Artemisia vallesiaca All., 2n=36

SWITZERLAND. Valais. Baltschieder, cliffs c. 200 m NNW of the village, c. 680 m (96). -- Conthey c. 1000 m SE, slope above Pont de la Morge, c. 570 m (98, 109). -- Gampel, slope c. 200 m west of the village, c. 670 m (95, 110). -- Granges c. 1000 m NE, near Clément, slope and cliffs c. 550 m (99, 111). -- Granges c. 1000 m NW, slopes along the road to Lens (159). -- Raron: slope and cliffs above the village, c. 670 m (97, 107); Slope near the church, c. 620 m (106). -- Saillon, slope above the village, c. 560 m (93, 105). -- Saillon c. 1400 m WNW, slope c. 550 m (108). -- St. Léonard, slope west of the village, c. 510 m (94, 103). -- Sion, Tourbillon, c. 700 m (92, 104). -- Sion c. 1500 m WSW, c. 550 m (158).

ITALY. Piemonte. Valle d'Aosta: Sarre, slope below the village near the main road, c. 620 m (112); Villeneuve, slope above the village, c. 690 m (100).

Artemisia santonicum L. ssp. santonicum, 2n=36

HUNGARY. Hajdu-Bihar. Near Debrecen (163 BG Debrecen).

ROUMANIA. Cluj. Near Cluj, Someşeni (157 BG Cluj). -- Turda (102 K. Brunsberg).

Artemisia santonicum L. ssp. santonicum, 2n=54

GREECE. Thraki. Xanthi, Porto Lago c. 4000 m WNW, salines (162).

Artemisia santonicum L. ssp. patens (Neillr.) K. Pers., 2n=18

AUSTRIA. Burgenland. Seewinkel: Apetlon c. 1500 m NNE, southern part of Xixsee (114); Apetlon c. 2000 m NE, eastern part of Xixsee (115); Illmitz c. 1200 m E (125); Langelacke, south-western corner (116); Oberstinkersee c. 100 m NE (113); Podersdorf c. 3000 m SE (126); Between Xixsee and Langelacke (117).

CZECHOSLOVAKIA. Slovensko. Nitra, Nové Zámky NW, Palárikovo (123 J. Šmiták).

Artemisia caerulescens L. ssp. caerulescens, 2n=18

PORTUGAL. Algarve. Lagos, near the river (135). -- Lagos NNE, near Odiáxere, east of the town near the river (136). -- Near Portimão, on the east shore of the Odelouca R. (137). -- Lisboa. Setubal c. 8000 m ENE, on the northern shore of the Rio Sado (134).

SPAIN. Huelva. Lepe c. 2000 m NE, on the shores of the Rio Piedras (138).

YUGOSLAVIA. Istra. Pula c. 1000 m S, rocky shore, in crevices (43). -- Pula c. 3000 m NW, near the road to Fažana, marsh and rock crevices near the marsh (44).

Artemisia caerulescens L. ssp. gallica (Willd.) K. Pers., 2n=18

FRANCE. Aude. Gruissan c. 4000 m WNW, near the southern road to Narbonne (142). -- Leucate c. 3000 m N, near the outlet of the Etang de Lapalme (140). -- Port-la-Nouvelle c. 2500 m NE, near the road to



Vieille Nouvelle (141). -- Bouches du Rhône. Camargue: Albaron c. 1000 m S (147); Arles S, on the western shore of the Rhône between Gageron and Villeneuve (148); Astouin (146). -- Fos-sur-Mer c. 2000 m W, near the sea (149). -- Hérault. Grau de Vendres (143). -- Mèze c. 2000 m WSW (145). -- Sérignan-Plage c. 500 m NNW (144). -- Pyrenées-Orientales. Along the eastern shore of the Etang de Canet et de St. Nazaire (139).





